2009

Concepts, theories and models of succession in the boreal forest of Central Canada

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CONCEPTS, THEORIES AND MODELS OF SUCCESSION IN THE BOREAL FOREST OF CENTRAL CANADA

by

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A Thesis Submitted in Partial Fulfillment of the Requirements for the Degree of

Doctor of Philosophy (Forest Sciences)

Faculty of Forestry and the Forest Environment

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ABSTRACT

Taylor, A.R. 2009. Concepts, theories and models of succession in the boreal forest of central Canada

Keywords: strategic planning, qualitative models, quantitative models, empirical models, mechanistic models, stand dynamics, competition, disturbance, fire cycle, regression, diversity; spruce budworm, tolerance

Predicting plant community compositional responses to changing environmental conditions and disturbances is a key element of forecasting and managing for the effects of global climate change. With advances in ecological modeling, many forms of succession models are available. Empirical-based succession models have been criticized as inflexible and limited by the quality and coverage of data for formulation; however, mechanistic models are tied to the underlying theory (quality and comprehensiveness) from which they are developed and make key limiting assumptions that the modeled processes they represent are adequately understood, thus underscoring the continual necessity for empirical testing of successional processes.

Currently, a great deal of our knowledge of succession in boreal forest is expert opinion-based or has been inferred from chronosequence studies. As a result, many commonly held assumptions on the nature and existence of succession in boreal forests are still debated. We, therefore, constructed a dataset of long-term repeated stand measurements, collected over a wide geographical area in central Canada, to test fundamental concepts and theories about boreal forest succession at the landscape and

tree population levels, including the existence of theorized multiple successional pathways and species population dynamics in the prolonged absence of stand replacing fire.

Overall, we observed a compositional shift over time, in which post-fire stands dominated by fast growing shade-intolerant species are eventually replaced by late seral, shade-tolerant species. This phenomenon, however, is not a simple unidirectional sequence of stages, but rather compositionally similar stands may exhibit multiple successional pathways dependent on differential species responses to physical site conditions, initial stand composition and intermediate disturbances. Individual species responses appeared largely controlled by shade-tolerance and regeneration strategy. We suspect these are the most important life history traits in explaining boreal forest succession.

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ACKNOWLEDGMENTS

I would like to give my sincere appreciation to my supervisor Dr. Han Chen for his help, support and guidance throughout the development of my thesis. I would also like to thank Rob Fleming, Lee Frelich, Gordon Kayahara, Laird Van Damme and Reino Pulkki for their constructive comments.

I thank Stan Vasiliauskas and Steve Hill for assistance in data collection. Support for this project was provided by Natural Science and Engineering Research Council (NSERC) of Canada, the National Centre of Excellence Network of Sustainable Forest Management, and the Ontario Living Legacy Research Program. I also would like to acknowledge NSERC and KBM Forestry Consultants Inc. for an Industrial Postgraduate Scholarship.

Thanks to my office mates, Brian Brassard and Meelis Seedre, for support and advice during writing my thesis and special thanks to my wife, Lisa Thomson, for her support and tolerance during those many hours spent working in the office.

CHAPTER ONE: GENERAL INTRODUCTION

Understanding long-term dynamics of vegetation composition is of increasing importance to ecologists and resource managers (Clark et al., 2001; Drescher et al., 2008), as it is linked with global climate change (Gower et al., 2001; Bond-Lamberty et al., 2007, Luyssaert et al., 2008; Canadell and Raupach, 2008), biodiversity (Franklin et al., 2002) and forest product supply (Harvey and Brais, 2002; Furst et al., 2007). The boreal forest is the largest terrestrial biome in the world and comprises nearly 90% of the productive forest area in Canada (Meillio et al., 1993; CCFM, 2000). Lightning-caused stand replacing fire is the dominant large-scale natural disturbance (Johnson, 1992), with fire cycle length varying regionally, but generally increasing from west to east (Weir et al., 2000; Lauzon et al., 2007).

To ensure continued provision of forest resources and ecological integrity, forestry in Canada has steadily evolved from sustained-yield management to ecosystem management (Armstrong, 1999; Kimmins et al., 2005). Successful implementation of ecosystem management requires strategic forest management planning (Davis et al., 2001). This includes the ability to forecast and evaluate forest succession over the span of the planning unit and horizon.

Defining 'succession' has become somewhat of a contentious issue as it is used to describe many types of vegetation change over widely varying temporal and spatial scales. Although many ecologists associate succession with change and the response to change in ecological systems, it is not sufficient to say succession only represents change, but that it implies a repeatable sequence of changes in vegetation composition over time

and space in which competition for limiting resources leads to the displacement of less tolerant species (Finegan, 1984; Tilman, 1985; van Andel et al., 1993).

With many advances in ecological modeling over the past several decades, forecasts of succession are now often undertaken using forest succession models (Johnsen et al., 2001; Messier et al., 2003). However, many of these models make key limiting assumptions i.e., that the underlying ecological processes they attempt to represent are adequately understood. Much of our current knowledge of boreal forest succession, and thus our ability to project succession for management purposes, is built-on expert opinion knowledge (e.g., Chen et al., 2001; Drescher et al., 2008). In fact, many commonly held assumptions on the nature and existence of succession in boreal forests, including the basic model of species replacement of shade-intolerant species by shade-tolerant species, are increasingly debated (Gutsell and Johnson, 2002; Johnson and Miyanishi, 2008). In part, because many contemporary studies are further revealing the complexity of long-term vegetation dynamics in boreal ecosystems (Chen and Popadiouk, 2002; Johnson and Miyanishi, 2008); but also, because much evidence of succession in boreal forest has been inferred from chronosequence (i.e., space-for-time substitution) methods. While useful in inferring general trends, the chronosequence approach is increasingly criticized for studying long-term vegetation dynamics since it makes the underlying assumption that all sites along the temporal sequence have developed similarly in their abiotic and biotic components (Johnson and Miyanishi, 2008).

This thesis comprises of three separate projects on the study of forest succession. The first project (i.e., Chapter Two) consists of a literature review on the various methods

of modeling forest succession and their contribution to forest management and research. Many past reviews of succession models have tended to focus on the development of specific types of models or provide historical accounts of debate between successional theories and mechanisms. Consequently, there is currently lack of a broad synthesis and description of the wide variety of methods used to model forest succession.

In the second and third projects (i.e., Chapters Three and Four, respectively) we use a dataset of long-term repeated stand measurements, collected over a wide geographical area in central Canada, to test fundamental concepts and theories about boreal forest succession, including those that have been inferred from previous chronosequence-based studies. Chapter Three examines succession at the landscape level by examining transitions in boreal forest stand types over time. Accordingly, we sought to test the following hypotheses: 1) In the long-term absence of stand replacing fire, compositionally similar stands may follow multiple successional pathways as stands age; 2) Multiple successional pathways may be related to edaphic conditions, which can influence overstory tree longevity, susceptibility to disturbances, and recruitment in the understory; and 3) Intermediate disturbances such as windthrow and outbreaks of forest tent caterpillar (*Malacosoma disstria*) and spruce budworm (*Choristoneura fumiferana*) may also influence successional pathways as they interact with stand age, site conditions, and stand composition.

Alternatively, in Chapter Four, we focused on studying succession at the tree species population level. Forest succession is commonly viewed as a community-level phenomenon, expressed through temporal changes in the abundance of plant species populations which comprise the community. Thus, our general objective was to test for

trends in individual species abundance over time. Specifically, we sought to test the following hypotheses: 1) Temporal shifts in boreal tree species composition are related to time since fire, characterized by decreases in the abundance of shade-intolerant species and increases in the abundance of shade-tolerant species over time; 2) Temporal trends in species abundance may differ with physical site conditions, since species relative competitive ability may be site specific; 3) Commonly occurring intermediate disturbances may alter trends in species abundance over time; and 4) Temporal trends in species abundance may differ depending on initial stand composition due to inter and intra species interaction effects.

Please note that because the projects in Chapters Three and Four were developed from the same field data, many of the data collection procedures described in their respective Materials and Methods sections are quite similar. Nonetheless, due to distinct differences in data treatment and analysis, these methods are repeated for each chapter.

CHAPTER TWO: A REVIEW OF FOREST SUCCESSION MODELS AND THEIR SUITABILITY TO FOREST MANAGEMENT PLANNING

2.1 INTRODUCTION

To ensure the continued provision of forest resources and ecological integrity, forestry has changed from sustained-yield management to ecosystem management (Armstrong, 1999; Kimmins et al., 2005). Successful implementation of ecosystem management requires strategic forest management planning (Davis et al., 2001). This includes the ability to forecast and evaluate future forest composition over the span of the planning unit and horizon.

Ecological research has long focused on understanding and predicting forest succession (e.g., Clements, 1916; Shugart et al., 1973; Pacala et al., 1996). Consequently, many forms of succession models are now available. Forest managers and novice modelers, who must evaluate and select among them face a challenging task. Qualitative modeling forms, although enriched in knowledge, require expression in more formal quantitative forms to be useful for strategic forest management planning (Locks, 1981; Harvey et al., 2002). Quantitative modeling methods vary in complexity and detail with their preference and application depending largely on end-use requirements (e.g., statistical accuracy and level of ecological realism) (Vanclay, 1994; Landsberg, 2003).

Past reviews of forest succession tend to focus on the development of succession models, providing historical accounts of debate between successional theories and mechanisms (e.g., Drury and Nisbett, 1973; Van Hulst, 1978; Finegan, 1984; Miles, 1987; Glenn-Lewin et al., 1992). Others have focused on the relative usefulness of models for understanding successional phenomena (e.g., Horn, 1981; Van Hulst, 1980;

Shugart, 1984; McCook, 1994). Some reviews have helped clarify the difference between various concepts and terminologies; notably, what defines a succession model, and its distinction from successional theories, mechanisms, and pathways (e.g., Pickett et al., 1987; Andel van et al., 1993).

There is currently lack of a broad synthesis and description of the variety of methods used to model forest succession. Shugart and West (1980) provide an early example of classifying succession modeling methods; however, two decades have passed since their review, along with advances in ecological modeling (Messier et al., 2003). A number of reviews classify forms of forest succession models, but these tend to focus on smaller subsets of models such as probabilistic models (e.g., Usher, 1992), gap models (e.g., Shugart, 1984; Huston, 1992; Urban and Shugart, 1992; Bugmann et al., 1996), or landscape simulation models (e.g., Keane et al., 2004; Scheller and Mladenoff, 2007). Reviews of forest growth models include examples of succession models, which are usually classified as a form of growth model and are not examined independently (e.g.,Vanclay, 1994; Peng, 2000; Porte and Bartelink 2002).

In this review, we provide a broad synthesis of methods used to model forest succession within a forest management planning context. We first identify the relevance of succession models in strategic forest management planning and outline criteria for evaluating their application. Next, we review succession modeling methods using the classification scheme outlined in Fig. 2.1. Review of each model class includes defining the modeling approach, providing examples, and discussing their suitability for strategic planning.

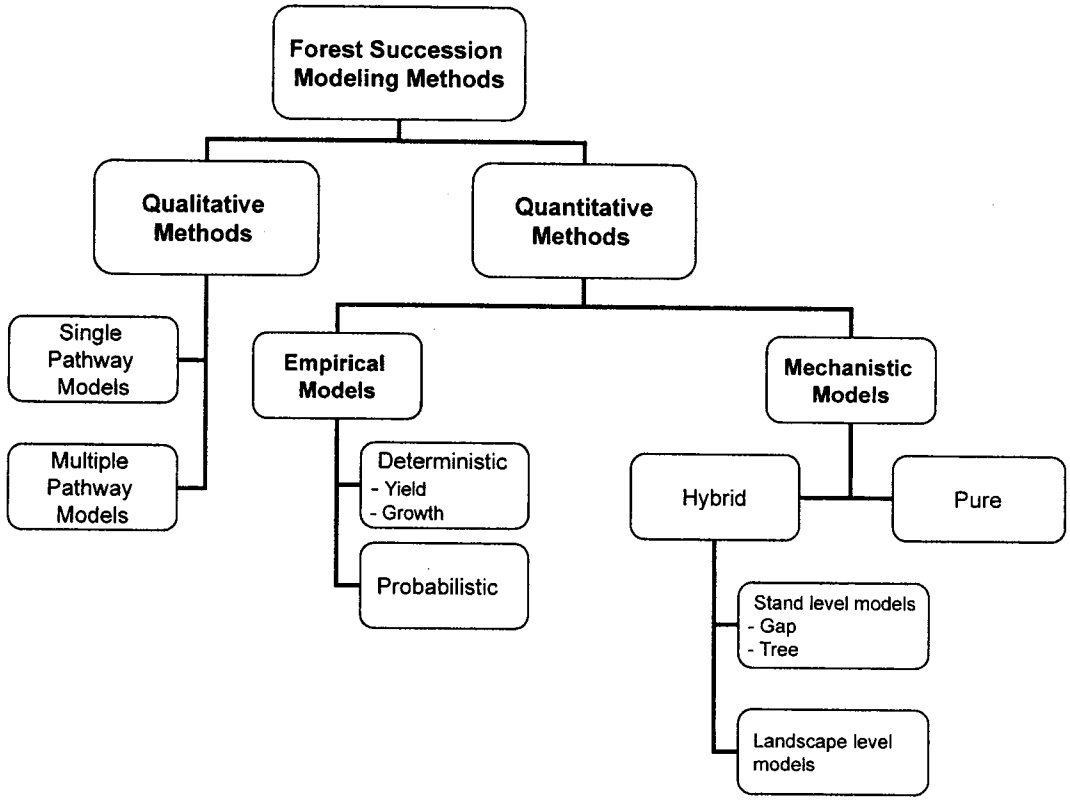

Figure 2.1 Classification scheme of forest succession modeling methods

2.2 SUCCESSION MODELS IN STRATEGIC FOREST MANAGEMENT PLANNING

Relevance of Succession Models

Ecosystem management emphasizes the maintenance of natural ecological conditions, within which, the sustained yield of products to meet human needs are achieved (Landres et al., 1999). Critical to successful ecosystem management is strategic level planning (Davis et al., 2001). This process includes defining the desired long-term objectives and developing, evaluating, and implementing management strategies to attain those objectives over the span of the planning unit (i.e., size of area to be analyzed) and horizon (i.e., length of time into the future that management activities are to be evaluated) (Davis et al., 2001). At the core of this process is the necessity to project future forest

conditions associated with specific management actions across multiple temporal and spatial scales (Korzukhin et al., 1996; Clark et al., 2001; Kimmins et al., 2005).

Projecting succession has become an increasingly relevant component of ecosystem management, as forest compositional change is linked to timber supply (Bergeron and Harvey, 1997), forest productivity and carbon sequestration (Pare and Bergeron, 1995; Martin et al., 2005), wildlife habitat suitability (Franklin et al., 2002), and social preference (Satake and Iwasa, 2006). Projecting successional trends for management purposes has historically been achieved through expert opinion (e.g., Chen et al., 2001; Davis et al., 2001). With advances in ecological modeling, forecasts of succession are often undertaken using forest succession models (Johnsen et al., 2001; Messier et al., 2003).

Assessing Model Suitability

The detail and accuracy of projection information required for strategic forest management planning may vary among management situations depending on the management objectives and dimensions of the planning unit and horizon (Davis et al., 2001; Stage, 2003). For this reason, evaluation criteria should be considered when assessing model suitability. We have outlined general criteria, derived from previous discussions on forest model evaluation (e.g., Buchman and Shifley, 1983; Vanclay, 1994; Stage, 2003), to assist in assessing the suitability of succession modeling methods for strategic forest management planning (Table 2.1). These evaluation criterions are described below, as well as generalized requirements for strategic planning.

Table 2.1 Summary of model evaluation criterion for strategic forest management planning.

Evaluation Criteria	Requirements and considerations for strategic planning
Input data	Must be compatible with data commonly available to management planning
Inference space	Planning horizon: 1-2 forest rotations ≈ 50-200 years Temporal resolution: 1-10 years Temporal capacity: must accommodate planning horizon
	Planning unit size: variable Small planning units (<1000 ha) tree/gap level resolution adequate Large planning units (>1000 ha) coarser resolution required
	Aspatial and spatial methods both acceptable and commonly used
	Quantitative reference to estimation accuracy and reliability required
Complexity	Ecosystem representation should be no greater than that essential to accurately project succession within desired inference space
	Unnecessarily complicated models incur extra cost
Flexibility	Ability to simulate alternative scenarios for comparison
	Adaptability for use under varying management and environmental conditions
	Output should be easily interpretable for planning analysis, and as input for planning models

Input data:

The type and amount of data required to formulize and to parameterize models can limit their usefulness and suitability in forest management planning. Many models require large databases or specialized measurements unattainable in some management situations (Vanclay, 1994; Stage, 2003). Ideally, data requirements should be compatible with data commonly available to forest managers such as growth and stand inventory information, usually derived from sample plots and aerial photography sources.

Inference space:

Forest management planning relies on stand inventory of the planning unit and forecasts of individual stand successional pathways. A stand is defined as a unit of forest area (typically several ha in size) containing a community of trees sufficiently uniform in species composition, age, and management type that it can be distinguished from forest in adjoining areas. Models, therefore, must provide estimates of succession for individual stands over time, with quantitative reference to estimation accuracy and reliability (Locks, 1981; Harvey et al., 2002).

A model's temporal and spatial resolution (i.e., smallest unit identified) and capacity (i.e., maximum projection limit without incurring intolerable error) should be harmonious with the inference space of the management situation under consideration (Landsberg and Coops, 1999; Groot et al., 2004). Inference space is defined by the dimensions of the planning unit and horizon. Typically, strategic level planning horizons consider 1 to 2 forest rotations, ranging from 50 to 200 years, depending on forest type, area, and management objectives (Davis et al., 2001). To facilitate such planning horizons, a model's temporal resolution should range from 1 to 10 years, allowing sufficiently low resolution to achieve strategic level forecasts, yet high enough to potentially support tactical planning periods (i.e., 5 to 10 years). The temporal capacity should allow forecasting succession over the length of the planning horizon (i.e., 50 to 200 years). Planning unit size may vary from an individual stand to thousands of stands. Suitable spatial resolution and capacity will therefore depend on the unique management situation. For smaller planning areas (i.e., 100s ha), tree level resolution may be suitable. For larger planning units (i.e., 1000s ha), coarser resolutions may be more appropriate.

Both aspatial and spatial modeling methods are acceptable in strategic planning situations. Spatial models are increasingly being used in management planning, a consequence of increased utilization of GIS technology (Martell et al., 1998; Landsberg, 2003) and the realization that spatial variables are important for understanding stand and landscape succession (Frelich and Reich, 1999; Augustin et al., 2001). Also, the ability to 'see' the modeled changes in the area being simulated is a valuable tool in planning, particularly for communicating forest management strategies to stakeholders (Turner et al., 1995).

Complexity:

Succession models developed for understanding the processes which lead to succession are generally research-orientated. Their bias towards ecological representation may therefore result in details and outputs unnecessary for planning purposes. Models less concerned with ecosystem representation may sacrifice ecological realism to achieve simpler models with fewer processes and higher statistical accuracy (Stage, 2003). The choice of modeling method should reflect whether extra details are required or if a simpler model could provide equally valid output. For strategic planning, model complexity need be no greater than that essential to accurately project succession within the desired inference space (Stage, 2003; Kimmins et al., 2005). Ecological phenomena governing forest change are scale dependent; structural dynamics at stand level scales are less apparent at the landscape level and may not be necessary to successfully model landscape level dynamics (Smith and Urban, 1988).

Flexibility:

Model flexibility refers to the ability to project forest succession under varying conditions and restrictions. Ecosystem management requires allowing for multiple environmental and social factors not traditionally considered under sustained-yield forestry. Some concerns associated with model flexibility for strategic planning under ecosystem management include: 1) Can the modeling method incorporate both natural and anthropogenic disturbance influences? 2) Can it simulate alternative management scenarios for comparison? 3) Is it easily adapted and/or recalibrated for use under different forest and environmental conditions? and 4) Can the model (or model's output) be easily integrated with other management planning analysis tools?

2.3 FOREST SUCCESSION MODELS

Concepts

Traditionally, vegetation succession refers to the directional change in plant species composition over widely variable temporal and spatial scales (Finegan, 1984). In their review, Pickett et al. (1987) proposed clarification in the literature of vegetation succession. They provided a framework that uses three main concepts to describe succession: pathways, mechanisms, and models. A successional pathway represents a temporal change in vegetation composition. It describes the transition of one stage of forest development to another. Successional mechanisms include those factors and causes (e.g., time, disturbances, and species' life history traits) that interact to drive successional pathways. Successional models represent conceptual maps that attempt to describe and to predict the direction of successional pathways by combining various mechanisms and specifying the relationships between the mechanisms and the stages of the pathway.

In its simplest form, a model is "an abstraction or a simplified representation of some aspect of reality" (Vanclay, 1994). In science, models are used to describe cause-effect relationships and to anticipate the behavior of systems. They take many forms (e.g., verbal or textual descriptions, diagrams, physical constructs, mathematical equations, or computer programs) and are used for a variety of purposes (e.g., describing processes, organizing data, and predicting future conditions). It is often incorrectly assumed that the use of computer programming is synonymous to modeling. It must be clarified that a computer is an important tool to help realize and implement a model, but is not necessarily central to the modeling process.

Although the attempt here is to make a distinction between the different methods of modeling forest succession, in practice, there is a virtual continuum of approaches, from the purely descriptive to the highly theoretical (Usher, 1992; Messier et al., 2003). Differences between approaches are not always apparent and some modelers intentionally combine modeling techniques. The broadest categorization of succession modeling methods begins with the distinction between qualitative or quantitative models (Fig. 1).

Qualitative Models

Qualitative models depict successional pathways by a diagram and a textual description of the mechanisms of influence (Usher, 1992; Yemshanov and Perera, 2003). The pathway(s) is reported as a sequence of discrete states without reference to quantitative measurement. Qualitative models represent the earliest attempts at modeling forest succession and can be generalized into two groups: single and multiple pathway models.

Single Pathway Models

The most basic forest succession models are textual conceptualizations that describe succession through a number of distinct stages. The classic example is the autogenic plant succession model based on Clements' (1916; 1936) monoclimax theory. It outlined an orderly-deterministic sequence of successive stages (nudation, migration, ecesis, competition, reaction) that follow one another in a linear fashion until a climax stage is achieved. A similar, more modern, example is the stand development model of Oliver (1981). It outlined four generalized stages of succession that describe plant community and environmental interactions, summarized as stages of stand development (stand initiation, stem exclusion, understory reinitiation, and old growth).

In response to the classic succession model, alternative qualitative models such as the 'Relay Floristics' and 'Initial Floristic Composition' models (Egler, 1954) arose that emphasized the role of individual species attributes and community interactions as the major drivers of succession. For example, some models focused attention largely on understanding plant resources, so that the biological drivers of importance in determining the course of succession were the physical stresses related to competition for resources between plants (see Drury and Nisbett, 1973; Horn, 1974). Later, Connell and Slatyer (1977) proposed a conceptual framework where mechanisms that drive succession could be summed and incorporated into three alternative models, defined as 'facilitation', 'inhibition' and 'tolerance'. These models have been applied to many studies with mixed results for describing succession (e.g., Debussche et al., 1982; Harris et al., 1984; Armesto and Pickett, 1986; Bergeron, 2000). While useful in explaining successional phenomena, they are not, in the strictest sense, models of succession, but rather

descriptions of successional mechanisms that focus on a specific aspect of the succession process, namely the mechanisms of species' turnover and replacement (Pickett et al., 1987).

Multiple Pathway Models

The single pathway approach to modeling succession provides a general framework of stages based on vegetative development. The duration and predictability of these stages, however, is not only dependent on species' attributes or community effects, but are inseparably linked to the sites and disturbance regimes to which they are adapted (Cattelino et al., 1979; Barnes, 1998). Single pathway models often deal with disturbances in general, with emphasis on replacement sequences observed in forest communities. Under "normal" conditions (e.g., regular fire periodicities), forest communities may follow a single regeneration pathway; yet, when subjected to very short or very long inter-fire periods, these successional pathways may part widely from the norm (Cattelino et al., 1979).

Succession is a multi-dimensional process driven by the interactions of autogenic and allogenic factors at various temporal and spatial scales and may best be described through multiple pathways. Multiple pathway models describe multiple outcomes of forest succession based not only on species attributes and community effects, but also on site conditions, disturbance types and severity, and time since disturbance. Early examples of these models include Olson (1958), and Cattelino et al. (1979). Cattelino et al. (1979) developed a multiple pathway model based on species replacement patterns following disturbances. Their model consisted of a schematic diagram illustrating the

multiple directions in which succession could occur in reaction to disturbance type and intensity, and individual species' life history traits.

In an attempt to summarize the types of multiple directions succession follows, Frelich and Reich (1995) derived five directional modes of succession from the literature (Cyclic, Convergent, Divergent, Parallel, and Individualistic), which together, comprised their multiple pathway model of boreal forest succession. Each proposed mode of succession considers various factors (biotic and abiotic) that lead to a defined pathway. They can be used simultaneously to formally describe the multiple successional pathways of a forest ecosystem. This is illustrated by Chen and Popadiouk (2002), who developed a multiple pathway model for boreal mixedwood forests in North America.

Applicability of Qualitative Models to Strategic Forest Management Planning

Qualitative forest succession models have formed the foundation for our current understanding of forest succession. The stand development model of Oliver (1981) can provide conceptual approximations of expected composition, function, and structure as forests develop. More complex, single pathway models have been developed which incorporate detailed scientific understanding of natural stand dynamics for specific forest regions (e.g., Chen and Popadiouk, 2002; Franklin et al., 2002). Of particular relevance to strategic planning has been their usefulness as guides of stand structural development to allow forest practitioners to make more informed management decisions.

Given the linear-deterministic nature of single pathway models, issues arise from their use, including unrealistic assumptions such as regional climate and disturbance regime will remain unchanged; the inability to incorporate stochastic events or alternative management strategies; and succession follows each stage in a linear-deterministic order.

In nature, disturbances often disrupt the gradual internal changes of ecosystems and re-direct or permanently change the successional direction (Cattelino et al., 1979).

Multiple pathway models lack the linear-deterministic dependency inherent to single pathway models and are able to incorporate a range of natural and anthropogenic influences. As a consequence, they can provide insight to possible forest transitions over time, depending on species vital attributes, disturbance regimes, or specific management strategies. However, similar to single pathway models, they lack any quantitative measure of performance or reliability of estimates. Their static nature (similar to an inventory) limits their flexibility and innovation to support the dynamism required as projection tools for strategic planning.

In conclusion, qualitative models, although enriched in knowledge, are limited in projecting succession for strategic forest management planning. They are best suited to describing empirical observations or theoretical hypotheses.

Quantitative Models

Quantitative models are those expressed through mathematical notation. They are typically dynamic in nature, with interacting state and system variables (Kimmins, 2004). The mathematical techniques in use vary in complexity, depending on the level of ecosystem detail the modeler desires to represent (e.g., a single equation or a series of interacting equations, which together comprise a simulation system).

To distinguish between the methods used to model succession quantitatively, it is helpful to first consider the intention of the modeling approach, i.e., is the purpose of the model to predict future forest conditions (management-orientated) or to understand processes (research-orientated) (Vanclay, 1994; Korzukhin et al., 1996). Models intended

for prediction purposes tend to sacrifice ecosystem representation to achieve more efficient and reliable outcomes (Stage, 2003). Model parameters are estimated by fitting mathematical functions to direct observation of forest development. Korzukhin et al. (1996) and Peng (2000) describe these models as empirical. Models for understanding typically include more detail of the underlying ecological relationships that cause forest development (Stage, 2003). They use fixed relationships based on theoretical knowledge, and parameters are estimated anew for different applications. Peng (2000) and Porte and Bartelink (2002) classify these models as mechanistic.

Empirical Models of Succession

Empirical succession models are developed from observation data of species compositional changes over time. The most commonly used strategy to model succession empirically is through the use of state-and-transition methods (Keane et al., 2004). Here, succession is represented at the stand or landscape level by linking successional stages along pathways of development. Each stage in the pathway represents a state which transitions into another. The transition from one state to another can be projected using either as Deterministic or Probabilistic approach.

Deterministic

Deterministic is when the outcome is not subject to chance, but determined by chain of causation (Vanclay, 1994). A deterministic empirical model of forest succession provides a specific estimate of species compositional change for a given set of initial conditions (i.e., stand species composition, regional climate, and edaphic characteristics). The most common approach is to reproduce successional changes in a community (a set of populations co-existing within a spatially delimited area) by modeling the dynamics of

species abundance and replacement, referred to as 'population dynamics' (Van Hulst, 1979; Usher, 1987; Van Hulst, 1992). Here, mathematical functions are used to describe the change of individual populations within a community to determine state-and-transition pathways. At the forest stand level, this may constitute modeling changes in the proportion of individual tree species over time. As the proportion of species changes, the stand composition transitions from one stand type into another, expressing a successional pathway.

In representing population dynamics, models have either yield architecture or growth architecture (Stage, 2003). Yield architecture methods typically use time (often expressed as stand age) as the controlling variable explaining population dynamics. The basic approach is adopting the simplest mathematical function applicable and fitting it to observed data of species abundance versus stand age to produce species' abundance curves over time (e.g., Bergeron, 2000; Yang et al., 2005). This is analogous to curve fitting (e.g., regression analysis) such as used in forestry to produce timber yield curves (Peng, 2000).

Yield methods for modeling population dynamics are descriptive, providing little explanation of the processes causing the trends being projected. Growth architecture methods, alternatively, utilize initial state variable conditions and systems of differential equations to control population dynamics through time. Although, individual species' abundance curves are expressed over a relevant time scale for interpretation, time is not the controlling variable. Rather, sequences in species abundances are generated for a set of populations within a community simultaneously. For instance, change in the abundance of one species within the community is interdependent on the simultaneous

change in abundance of all other species being considered. Van Hulst (1979) used this method to examine the effects of various successional mechanisms on pathways, including resource competition between populations. The usage of differential equations as stand-alone models to simulate succession was most common during the 1970s and early 1980s. Since then, with the advancement of personal computers, little work has been published which solely uses these equations to model succession. This is largely because the explanatory capabilities that differential approaches provide can be facilitated in a mechanistic manner using computer simulation models, such as the evolving family of 'tree' and 'gap' mechanistic models, discussed later.

Probabilistic

Probabilistic models are the most common empirical modeling method published in the scientific literature. They are primarily used to estimate the transition probability of a successional state to remain the same or change into another over time. The most widely used approach for estimating transition probabilities is by Markovian chain theory (e.g., Bellefleur, 1981; Acevedo et al., 1995; Yemshanov and Perera, 2002). Unlike deterministic models that focus on the population dynamics of individual entities (e.g., species) in determining the state and transition of a community, Markovian models focus on the state of the community and the probability of the community's state remaining the same or transitioning into another (Usher, 1987). From a population dynamic perspective, succession is a continuous change in species abundance; succession from one state to another is dependent on the change in individual species abundances. Markovian models, alternatively, assume the continuum is divided into a number of discrete finite states.

Each state is characteristic of a successional stage or cover type, usually based on species dominance.

The literature is full of examples where Markovian models have been used to study and estimate the sequence of vegetation change. During the 1970s – 80s, Markov models gained attractiveness as practical alternatives to systems of differential equations and more sophisticated tree and gap mechanistic models (Shugart, 1984). Two early and commonly cited examples, based on sets of long-term empirical data, are that of Watt (1960) and Waggoner and Stephens (1970). Since then, many succession applications of Markovian models have been developed (see Horn, 1975; 1981; Usher, 1981; 1992; Yemshanov and Perera, 2002).

From a practical point of view, transition probabilities can be used to portray, diagrammatically, how succession in a system of states being studied is occurring (Usher, 1992; Acevedo et al., 1995). Some qualitative models, such as multiple pathway models, could have a quantitative-probabilistic element added by integrating a matrix of transition probabilities. An emerging modeling alternative that may provide more explanatory power in estimates of transition probabilities is multinomial logistic regression (Agresti, 1990). Augustin et al. (2001) and Rutherford et al. (2007) used this technique to explore the influence of explanatory variables in predicting the successional pathways of vegetation types in Scottish grasslands, and land cover successional patterns on abandoned agriculture land in Switzerland, respectively.

Applicability of Empirical Succession Models to Strategic Forest Management Planning

Empirical modeling approaches require simple input data, fewer parameters to estimate, and are computationally less complex in comparison to mechanistic methods (Korzukhin et al., 1996; Peng, 2000). They do, however, require much multi-temporal data to be developed and validated (Yemshanov and Perera, 2002). Deterministic yield methods and probablistic approaches require multi-temporal data of species compositional change. These data can be acquired through the observation of repeatedly measured sample plots (e.g., Archambault et al., 2006), chronosequence data (e.g., De Grandpre et al., 2000), historical records such as repeated aerial photographs (e.g., Frelich and Reich, 1995; Cumming et al., 2000), or dendrochronological techniques (e.g., Bergeron, 2000). Sample plot data and aerial photographs are commonly used in forest management in developing forest inventories and growth and yield curves. Pre-existing data could support the development of locally derived empirical succession models without imposing impractical data acquisition cost.

Data requirements of differential equations are more extensive. Calibration of the Volterra-Lotka competition equations (Van Hulst, 1979), for instance, requires empirical measurement of each species population growth as a function of the abundance of all other species present in the modeled community (Van Hulst, 1979; Pacala et al., 1996). Such atypical data is expensive to acquire and may not be practical for strategic planning purposes.

Empirical modeling approaches provide concise straightforward estimates of forest succession. Outputs, such as species abundance curves or transition probabilities,

are generally easily interpreted by forest practitioners. They can be used to directly estimate the successional pathways of individual stands, or as stand succession rules for input into management planning models, e.g., SFMM (Chen et al., 2001) and Patchworks (SPS, 2004). Statistical techniques applied in both deterministic and probabilistic models (e.g., regression analysis) generally provide measures of statistical accuracy and reliability of estimates.

Empirical models can be developed to project succession over a full range of temporal and spatial scales and are limited primarily by the extent of data available for formulation. Population dynamic-based models are most suited to represent within-stand species dynamics (e.g., Van Hulst, 1979; Bergeron, 2000; Yang et al., 2005), but larger resolution landscape models have also been developed (e.g., Shugart et al., 1973). Similarly, Markovian models have been developed at multiple scales. Early tree models of succession were empirically-based. The recruitment and replacement of individual trees within a defined area was modeled as a Markovian process using matrices of tree-by-tree transition probabilities (see Horn, 1981). Markovian models are well suited to landscape scale management because stands or larger forest units can easily be delineated to represent discrete states in the model. The concise quantitative information they provide (i.e., the probability that a stand will have a certain forest composition after a specific time period) is straightforward from a management perspective.

In terms of spatial capacity, most empirical models are developed aspatially. Spatially related explanatory variables, however, can be included to account for spatial influences acting on succession, e.g., proximity to seed source, stand size, and forest-edge shade effects (Augustin et al., 2001; Dovciak et al., 2005). Augustin et al. (2001)

observed that the ability to incorporate spatial variables, using multinomial logistic regression, improved the reliability of estimated transition probabilities. A number of spatially explicit landscape simulation models include empirical succession models as sub-models in their construct to provide successional capacity. Output from the empirical sub-model is used in conjunction with a GIS to project the succession of individual forest units on the landscape (e.g., Hargrove et al., 2000; Perera et al., 2003; Rammig et al., 2006).

Empirical models demonstrate their strength in describing the best-fit relationship between the measured data and the independent variables (Peng, 2000). Due to the straightforward formulation and dependence on empirical data, the use of empirical models for predicting complex ecological processes, such as forest succession, has sometimes been criticized as being too simplistic (Wootton, 2001; Messier et al., 2003).

Forest succession dynamics take place over long-time periods, thus the available data from which to infer useful empirical succession models are limited (Finegan, 1984; Bergeron, 2000). Because these models are usually derived from historical data, they assume how the forest developed in the past is how it will develop in the future. This may limit their usefulness to predicting succession over timescales for which historical growth conditions are not expected to change. While empirical models developed for a particular forest site or region may be adapted or calibrated to some extent to simulate succession under alternative management and environmental conditions, their usefulness and flexibility ultimately depends on the coverage of data available.

Mechanistic Models of Succession

Mechanistic models (sometimes referred to as ecosystem or process-based models) simulate ecosystem phenomena through interacting series of equations and algorithms. Mechanistic models simulate succession by modeling the underlying ecological processes of causation. Due to the complexity of the processes they attempt to represent, mechanistic models are realized as computer simulation models. Depending on the system approach they use to carry out the simulation process, a distinction can be made between pure and hybrid mechanistic models (Peng, 2000; Kimmins, 2004). Pure mechanistic models are those developed to simulate ecosystem change based on physical and physiological principals instead of empirical input-output relationships (Landsberg and Gower, 1997). Highly parameterized models model photosynthesis, transpiration, and nutrient utilization at the scales of individual leaves in the canopy, at hourly and daily time steps, e.g., BIOMASS (Mcmurtrie and Landsberg, 1992) and MAESTRA (Medlyn et al., 2005; Ibrom et al., 2006). Mechanistic models that attempt to model forest growth at larger spatial and temporal scales tend to become less complex and more reliant on empirical relationships, e.g., PROMOD (Battaglia and Sands, 1998) and 3PG (Landsberg and Waring, 1997; Landsberg et al., 2005).

The strength of pure mechanistic models lies in their explanatory and descriptive ability as a research tool. They are not suited, nor necessarily intended, to be predictors of forest succession, particularly at the temporal and spatial scales required for strategic planning. For review of this modeling approach and its application to forest management, see Landsberg and Gower (1997) and Landsberg and Coops (1999).

Hybrid Models

Hybrid mechanistic models couple empirical modeling techniques with a process-based approach (Peng, 2000). Elements of ecosystem processes that are described and represented by empirical relationships (e.g., growth equations), are modified and interact in a mechanistic manner. Major drawbacks, such as data dependency and flexibility issues with empirical models or excessive complexity in pure mechanistic models, are balanced by combining the two approaches (Landsberg and Gower, 1997). For predicting forest succession, hybrid models have been developed at both the Stand level and Landscape level.

Stand level models

Stand level hybrid models of forest succession are comprised primarily of 'gap' models and 'tree' models, wherein the basic units used to simulate forest dynamics are individual trees (Munro, 1974; Shugart and West, 1980; Houllier, 1995). However, while gap models simulate the dynamics of individual trees, the trees are modeled aspatially and within a restricted spatial unit referred to as a gap. Although individual trees are considered as part of the model's formulation, they contribute in an aggregate manner to characterize a homogeneous gap. A mosaic of these gaps is then used to describe the forest stand or landscape of interest.

Gap models descending from the original JABOWA-FORET (Botkin et al., 1972; Shugart and West, 1977) model design include interacting sub-models which simulate the recruitment, growth, and death of individual trees within each gap. In JABOWA, the gap size corresponds to the crown area of a large mature tree, typical of hardwood forests in the north-eastern USA (Botkin et al., 1972; Botkin, 1993). Most gap models today

simulate gap sizes that vary between 100 to 1000 m^2. In the majority of gap models the canopy is represented as a homogenous layer of foliage across the entire gap; meaning, there is no horizontal spatial representation of individual trees. Rather than direct tree-to-tree interactions, individual trees modify the conditions of the gap which in turn influence neighboring trees. There have been, however, gap models developed that provide some spatial representation, e.g., SPACE (Busing, 1991) and ZELIG (Smith and Urban, 1988; Larocque et al., 2006). ZELIG utilizes a two-dimensional grid of cells (i.e., gaps) to represent the forest canopy. Theoretically, the trees in each cell influence the availability of resources to trees in adjacent cells. While individual trees within each cell are affected by adjacent cells, direct tree-to-tree interactions are still not captured.

Tree models simulate the dynamics of a stand or landscape by modeling the individual trees that comprise the area, without the intermediate gap step. Tree models are considered either as distance-independent or distance-dependent. Distant-independent models treat individual trees aspatially, while distant-dependent models take into account the relative position of each tree in the area being simulated. Prognosis (Stage, 1973) is one of the earliest examples of a hybrid tree model and has formed the basis from which a number of modern distance-independent tree models have developed, e.g., PROGNAUS (Monserud and Sterba, 1996), and Forest Vegetation Simulator (FVS) (Teck et al., 1996; Crookston and Dixon, 2005). Its development was facilitated by the USDA to provide improved quantitative understanding and prediction of stand development in pure and mixed forests under alternative management regimes through integration of known silvicultural knowledge and empirical tree growth data. Prognosis's modern version, FVS, represents an amalgamation of the original Prognosis model with

various model extensions developed over the years to enhance representation of stand characteristics, e.g., understory vegetation, wildlife habitat, and disturbance influences. It is extensively used throughout the US to support strategic level forest management planning and includes 22 variants calibrated to specific geographical areas (Crookston and Dixon, 2005). FVS has been linked with GIS and visualization systems to add spatial and visual capacity to its simulation outputs. Individual trees however, are still modeled aspatially thus maintaining the model's distance-independent nature.

The response to demand for more detailed spatial representation in simulating forest growth and succession brought about the development of distance-dependent tree models. The model FOREST (Ek and Monserud, 1974) is an early example developed to study northern US hardwood forests. It emphasized spatial competition interactions between individual trees and their influences on tree growth and mortality. Output was provided as periodic stand tables of timber yield and mortality information. SORTIE (Pacala et al., 1993; Pacala et al., 1996) is a contemporary and spatially explicit example of a distance-dependent tree model. SORTIE's modeling framework stems from the basic gap approach; it, however, simulates the competitive relationships between individual trees within a spatial community using a two dimensional co-ordinate system. Each tree in the model is represented by x, y coordinates and directly interacts with neighboring trees.

In SORTIE, many of the functions associated with the growth, mortality, and recruitment sub-models consists of species-specific equations which have been empirically parameterized and validated (Pacala et al., 1996; Papaik and Canham, 2006), uncommon to many JABOWA-FORET type gap models. SORTIE was originally

developed to study successional dynamics in oak-northern hardwood forests in northeastern North America. It has since been adapted and applied to a number of forest types. SORTIE/BC (Coates et al., 2003) is a version of the original SORTIE that has been parameterized and extensively modified to study silvicultural applications in British Columbia. Papaik and Canham (2006) have integrated an empirically based model of wind throw disturbance, seed-mass dispersal, and recruitment into SORTIE to study the effects of species-specific resistance and recovery from wind disturbance on successional trajectory.

Landscape level models

As the role of large scale disturbances on landscape dynamics has been more recognized (Johnson, 1992), broad scale representation of forest landscape dynamics for implementation of ecosystem management has become increasingly relevant (Korzukhin et al., 1996; Perry and Enright, 2006). Landscape models use a combination of empirical relationships and mechanistic processes to project forest succession. They generally operate at larger temporal and spatial resolutions. Time steps can be 10 years or greater and minimum spatial units range from 10s of m^2 to 100s of ha in size. Due to their coarse temporal and spatial resolution, forests are typically represented in an aggregated manner as forest area units or cells characterized by species composition, age class or management type. Because the study of landscape ecosystem dynamics is highly associated with spatial heterogeneity, many landscape level models are spatially explicit. Modern examples are often developed in association with GIS. Due to the stochastic nature of natural disturbances, landscape models use stochastic mechanisms extensively as part of their simulation process (Perry and Enright, 2006).

One of the well-known spatial landscape models is LANDIS (Mladenoff et al., 1993; Mladenoff and He, 1999; Scheller et al., 2007). It has been developed to simulate forest ecosystem dynamics at broad spatial resolutions with relatively few parameters to allow ease of use and adaptability (Mladenoff, 2004). Like similar landscape models of its type, e.g., DISPATCH and REFIRES (Davis and Burrows, 1994), emphasis was placed on incorporating major disturbance types and their stochastic nature. LANDIS forecasts landscape level successional dynamics through simulating species establishment and replacement within cells on a two-dimensional grid. Forest cover change in each cell is influenced by species-specific vital attributes, local climate and site conditions, and disturbance regimes. Conceptually, the model's structure can be considered as a map of grid cells on the landscape where each grid cell contains information on the tree species present and their respective age-class. A series of associated GIS layers in the model provide each grid cell with climate, soil, topography, and disturbance information.

Other landscape modeling approaches that have been developed based more firmly on empirical structure include EMBYR (Hargrove et al., 2000) and BFOLDS (Yemshanov and Perera, 2002; Perera et al., 2003). As an alternative to modeling vegetative succession based mainly on species-specific tree level dynamics and community processes, both use empirically-based probabilistic sub-models to provide successional capacity. For example, forest cover persistence and transition in BFOLDS is primarily governed by a time-dependent semi-Markovian model (Yemshanov and Perera, 2002). Discrete states (i.e., forest cover types) in the model are defined by tree species dominance. The semi-Markovian model calculates the time-dependent transition probability of the forest cover type in each grid cell to remain the same or transition. In a

case study of BFOLDS (Perera et al., 2003), transition probabilities were developed from a combination of multi-temporal empirical data and expert opinion.

Application of Hybrid Models to Strategic Forest Management Planning

Hybrid models are increasingly being applied to forest management planning (Johnsen et al., 2001). The intensity and type of input data required by hybrid models varies widely, depending on their spatial resolution, capacity, and the detail in which ecosystem processes are represented. Stand level models simulate the dynamics of every single tree. For management of smaller areas (<1000 ha) this approach may be suitable. For larger areas (1000's ha) these models are costly in terms of initialization data, computing power, and time (Pacala et al., 1996; Mladenoff, 2004). Distance-dependent tree models such as SORTIE and its variants (e.g., Coates et al., 2003; Papaik and Canham, 2006) not only require empirical data to develop parameters for the recruitment, growth, and mortality of every tree and species present, but also reference information concerning the location of each tree in the simulated area. Data of individual tree co-ordinates is not typically available and probably unattainable for large areas. Distance-independent tree models lack spatial dependency, so less intensive initialization data is required. Consequently, their use for planning purposes is the most common among gap and tree models, e.g., FVS (Crookston and Dixon, 2005). While data requirements range among landscape models, their input needs are more compatible with data generally available for management of larger planning units. This is because the low spatial resolutions they operate at are more practical in representing the stand-size polygons typically considered in strategic planning, and much of the initialization data required can

be obtained from GIS information commonly available for planning purposes (e.g., Perera et al., 2003; Scheller et al., 2007).

Hybrid models offer several advantages over empirical modeling techniques for strategic forest management planning; the foremost being their flexibility for scenario planning, a key component of decision-making (Davis et al., 2001). Unlike empirical models, hybrid models are less restricted to site-specific conditions and can be re-parameterized or modified to deal with changes in management and environmental conditions. The tree model FVS has been locally adapted to various geographical regions within the US and Canada to provide strategic forest management support (Crookston and Dixon, 2005). Species autecology and site condition data were obtained from published and expert opinion sources to parameterize LANDIS-II to study boreal forest management in Manitoba, Canada (Scheller et al., 2007).

Due to their more descriptive representation of ecosystem dynamics and decreased dependency on observed data, hybrid models can be configured to simulate a wide range of natural and anthropogenic influences on succession and project the consequences over relevant time scales, allowing for testing of complex hypothesis (Korzukhin et al., 1996; Gustafson et al., 2000; Kimmins, 2004). For example, the gap models FORSKA-2 (Prentice et al., 1993), LINKAGES (Wullschleger et al., 2001) and FORCLIM (Shao et al., 2003) have been used to assess the impacts of climate change on stand succession and productivity. ZELIG was implemented by Hansen et al. (1995) to explore the impact of various forest harvesting techniques on economic activity and habitat suitability in Pacific Northwest forests in the US. Many published examples (see Perry and Enright, 2006) demonstrate the usefulness of modern landscape simulation

models for studying the effects of climate change and alternative management strategies on forest landscape dynamics.

Increasingly, the management of multi-cohort mixedwood forests is relevant as ecosystem management systems attempt to maintain biological diversity and productivity (Groot et al., 2004). Trees of different sizes and species vary in growth, mortality, and regeneration characteristics. Gap and tree models are capable of incorporating size and species-specific growth and mortality functions, allowing for the simulation of multi-cohort mixed-species stands. This capacity is not necessarily shared with empirical modeling methods and some coarse-resolution landscape models (e.g., Kurz et al., 2000; Li, 2000; Perera et al., 2003) that tend to average parameter values out over the entire stand or community (Urban and Shugart, 1992).

Because hybrid models project succession based largely on mechanistic relationships, they present several challenges for strategic planning. First is the degree of complexity to represent numerous ecological processes. Each addition to a model exponentially increases the difficulty of testing and calibrating it (Rykiel, 1996). Excessive complexity may incur several costs: 1) greater computational cost; 2) loss in precision of estimates; and 3) difficulty in understanding and assessing the utility of the model (Vanclay, 1994; Korzukhin et al., 1996). Bugmann et al. (2001) noted that tree models such as SORTIE and FIRE-BGC (Keane et al., 1996) were too complex to be adapted to new forest ecosystems without significant research efforts. Such efforts may not be realistic under management constraints (i.e., time and money). Models with large numbers of parameters have limited usefulness to managers who have neither the time,

skills, nor tendency to seek sensible values (Landsberg and Coops, 1999; Landsberg, 2003).

While hybrid models are considered more ecologically realistic, they make key limiting assumptions, i.e., that the underlying ecological processes they attempt to represent are adequately understood. Although the usefulness of empirical models is limited by the quality and coverage of data for formulation, mechanistic models are tied to the underlying theory (quality and comprehensiveness) from which they are developed. Ecological relationships simulated in many gap and tree models, for instance, often lack empirical validation since long-term observed data often does not exist for comparison (Landsberg, 2003; Perry and Enright, 2006). Whether the theoretical relationships modeled hold across all stand types over the long-time scales desired for strategic planning becomes questionable. Lack of published data relating growth and mortality, for example, has led to the use of generalized growth-dependent mortality functions that are applied to all species. Significant inter-specific differences between mortality sub-models has, however, been demonstrated (Pacala et al., 1996). Such generalizations can have large consequences on species replacement sequences throughout succession, effecting confidence in model projections.

2.4 CONCLUSION

Successful ecosystem management requires strategic forest management planning, including the ability to project and to evaluate future forest conditions over the planning unit and horizon. Projecting forest succession has become an increasingly relevant component of ecosystem management. Historically, forecasting successional trends for management purposes was achieved through expert opinion and experience;

however, with advances in ecological modeling forecasts of succession are often undertaken using forest succession models.

Qualitative methods are diagrammatic and textual and report succession as a sequence of states without quantitative reference of estimates that are required in strategic forest management planning. Quantitative methods can be differentiated as empirical or mechanistic. Empirical models rely on observational data of succession and seek to describe successional patterns among the empirical data. Mechanistic models, alternatively, focus on underlying ecological processes and simulate succession by modeling the processes that lead to ecosystem change rather than the change itself. Hybrid mechanistic models represent a compromise in ecological modeling between empirical robustness and theoretical understanding. Relative to pure mechanistic modeling forms, they are more suited for strategic forest management planning. Advantages and disadvantages of empirical versus hybrid modeling methods are summarized in Table 2.2.

Both empirical and hybrid models have been used to project succession for strategic forest management planning. Because ecosystem management requires managing for multiple environmental and social factors, not traditionally considered under sustained-yield forestry, hybrid models are well suited because of their increased flexibility for scenario planning and enhanced representation of ecosystem processes. However, empirical models still remain a suitable and practical alternative since hybrid models require increased resources to initialize, operate, and interpret; emphasize understanding rather than prediction; and assume that the modeled processes they represent are adequately understood. We conclude that there is no single best modeling

approach for strategic forest management planning. Choice of model is ultimately dependent on the resources available for model formulation and validation, and the level of detail and accuracy required for individual management situations.

Table 2.2 Comparison of empirical vs. hybrid modeling methods.

Evaluation criteria	Empirical	Hybrid
Input data	Multi-temporal data of species compositional change	Parameters of species traits and ecosystem processes Inventory data Site conditions data
Inference space:		
Resolution	*Deterministic models:* ≥ 1 year time steps Individual populations (e.g., species, stand types) within a community (e.g., stand or landscape) *Probabilistic models:* ≥ 1 year time steps Discrete states (e.g., trees, stands, forest units) of a community (e.g., stand or landscape)	*Stand level models:* 1-10 year time steps Trees or gaps/cells (10^2-10^3 m^2) *Landscape level models:* ≥ 1 year time steps Forest units/cells ($10m^2$-100 ha)
Capacity	Limited by quality and coverage of data Typically aspatial, but can include spatial variables	*Stand level models:* 50-300 years 10^2-10^3 ha *Landscape level models:* 50-500 years 10^3-10^6 ha Aspatial and spatial available for both
Complexity	Low to intermediate	Intermediate to high
Flexibility	Low to intermediate	Intermediate to high
Key Advantages	Fewer parameters Data requirements generally compatible with management Efficient and easy to understand	More easily re-calibrated for alternative management and environmental conditions Greater flexibility for scenario planning and hypothesis testing Greater ecosystem representation
Key Disadvantages	Usefulness limited by extent of empirical data Limited representation of successional mechanisms	Many parameters to estimate Assumes modeled processes are adequately understood Limited empirical data available to verify processes and long-term predictions

CHAPTER THREE: MULTIPLE SUCCESSIONAL PATHWAYS OF BOREAL FOREST STANDS IN CENTRAL CANADA

3.1 INTRODUCTION

Understanding plant community compositional responses to global change is a key challenge for ecologists and resource managers (Clark et al., 2001; Bond-Lamberty et al., 2007; Ibanez et al., 2009). Climate change effects on wildfire frequency are expected to vary across the North American continent (Flannigan et al., 2001; Flannigan et al., 2009). In parts of the boreal forest the fire cycle has increased over the past century due to a less conducive climate and human-related fire suppression activities (Bergeron et al., 2001; Flannigan et al., 2001). Knowledge of successional direction in the prolonged absence of stand-replacing fire is important as the demographic of the landscape transitions to older forest.

Immediately following stand-replacing disturbance, multiple successional pathways may arise as a result of type and intensity of stand-replacing disturbance, local physical site conditions and pre-disturbance stand composition (Cooper et al., 2003; Dovciak et al., 2005; Johnstone and Chapin, 2006; Chen et al., 2009; Donato et al., 2009). In the prolonged absence of stand-replacing disturbance, boreal ecosystems continue to undergo secondary succession as dominant tree species of the post-disturbance cohort senescence and may not be capable of self-regenerating in the understory (Frelich and Reich, 1995; Bergeron, 2000) or because intermediate disturbances such as wind, insects or disease selectively kill part of the stand, resulting in changes in overstory composition (Bouchard et al., 2006; Rich et al., 2007).

Similar to post-disturbance succession, multiple successional pathways may also occur as stands age in the absence of stand-replacing disturbances (Frelich and Reich, 1995; Chen and Popadiouk, 2002; Caplat and Anand, 2009). The theory of 'multiple successional pathways' in ageing stands was conceptualized by Cattelino et al. (1979) as a 'process-based' alternative to the classical linear-deterministic approach (e.g., Clements, 1936) to succession in disturbance-prone systems. Corresponding with recent shifts in community ecology towards unified neutral theory (Holt, 2006; Clark, 2009), models of succession have come to rely on stochastic forces as key explanatory mechanisms of successional direction, whereby multiple pathways are largely considered the result of stochastic events (e.g., fluctuations in seed dispersal and mortality rates). Conversely, critics of neutral theory point out that there are no theoretical or empirical bases for stochasticity in nature, just unexplained variance in models, and suggest a return to focusing on deterministic mechanisms driving vegetation dynamics (Mcgill et al., 2006; Clark et al., 2007).

Within a bioclimatic region, predicting successional pathways may best be achieved through a better comprehension of the interactions between local plant species (e.g., species life history traits and neighborhood effects), site conditions (e.g., physiography, edaphic conditions) and natural disturbance regimes (Frelich and Reich, 1999; Lecomte and Bergeron, 2005; Bouchard et al., 2006; Caplat and Anand, 2009). However, few studies have tested multiple successional pathways in ageing stands directly with empirical data. Lack of progress in this area may be attributed to the commonly used chronosequence (space-for-time substitution) and stand reconstruction approaches to studying forest succession. The chronosequence approach inherently

assumes one or more successional pathways along the temporal sequence constructed. Further, it implies that all sites sampled along the temporal sequence have developed similarly in their abiotic and biotic components (Brassard et al., 2008; Johnson and Miyanishi, 2008). Dendrochronological reconstruction (e.g., Johnson et al., 1999; Bergeron, 2000) is too costly to permit sampling a sufficient amount of stands to test for multiple pathways. Alternatively, sequential aerial photography in combination with ground survey measurements is increasingly being considered as an important source of empirical data for studying long-term temporal trends in vegetation composition over large spatial contexts (e.g., Frelich and Reich, 1995; Bouchard et al., 2006). In conjunction, multinomial logistic regression has emerged as valuable statistical tool for analyzing spatial and temporal patterns of vegetation cover change (Augustin et al., 2001; Rutherford et al., 2007). It permits modeling probabilities of discrete outcome states originating from a single starting state, conditional on a set of explanatory variables.

In this paper, we develop a methodology for studying multiple successional pathways in boreal forest stands using repeatedly measured data derived from sequential aerial photographs and ground surveys. Because of the dominant role of the overstory on successive vegetation dynamics, we modeled successional pathways based on initial stand types that are classified by the dominance of overstory tree species. Using multinomial logistic regression to analyze stand type transitions, we sought to test the following hypotheses: 1) Compositionally similar stands may follow multiple successional pathways depending on time since last stand-replacing fire as it relates to neighborhood effects, i.e., processes mediated by overstory trees that affect the probability of self-replacement or invasion by other species at time of canopy mortality

(Frelich and Reich, 1995; Kneeshaw and Bergeron, 1998; Frelich and Reich, 1999), including alteration of the understory light environment and forest floor properties which may facilitate or inhibit establishment of a given species; 2) Multiple successional pathways may also be related to local edaphic conditions, which can influence overstory tree longevity, susceptibility to disturbances, and recruitment in the understory (Robichaud and Methven, 1993; Lecomte and Bergeron, 2005); and 3) Intermediate disturbances such as windthrow and outbreaks of forest tent caterpillar (*Malacosoma disstria*) and spruce budworm (*Choristoneura fumiferana*) may set back, accelerate, or permanently change the course of succession as they interact with stand age, local site conditions, and stand composition (Kneeshaw and Bergeron, 1998; Bouchard et al., 2006; Rich et al., 2007).

3.2 MATERIALS AND METHODS

Study area

Our study was located in region 3E (Hills, 1960) in northeastern Ontario, Canada (Fig. 3.1). Mean annual temperature is 1.3°C and mean annual precipitation is 831 mm (Canada Climate Normals 1971-2000, Timmins). Dominant tree species include *Pinus banksiana*, *Populus tremuloides*, *Populus balsamifera* (L.), *Betula papyrifera*, *Picea mariana*, *Picea glauca*, *Abies balsamea*, and *Thuja occidentalis*. The dominant stand-replacing natural disturbance is high-intensity crown fires. In areas adjacent to our study, Bergeron et al. (2001) observed a general increase in the fire cycle since the mid-19th century and found the average fire cycle, since 1920, to be > 190 years. Other important natural disturbances include windthrow, and insect infestation by spruce budworm (SBW) and forest tent caterpillar (FTC) (Fleming et al., 2002).

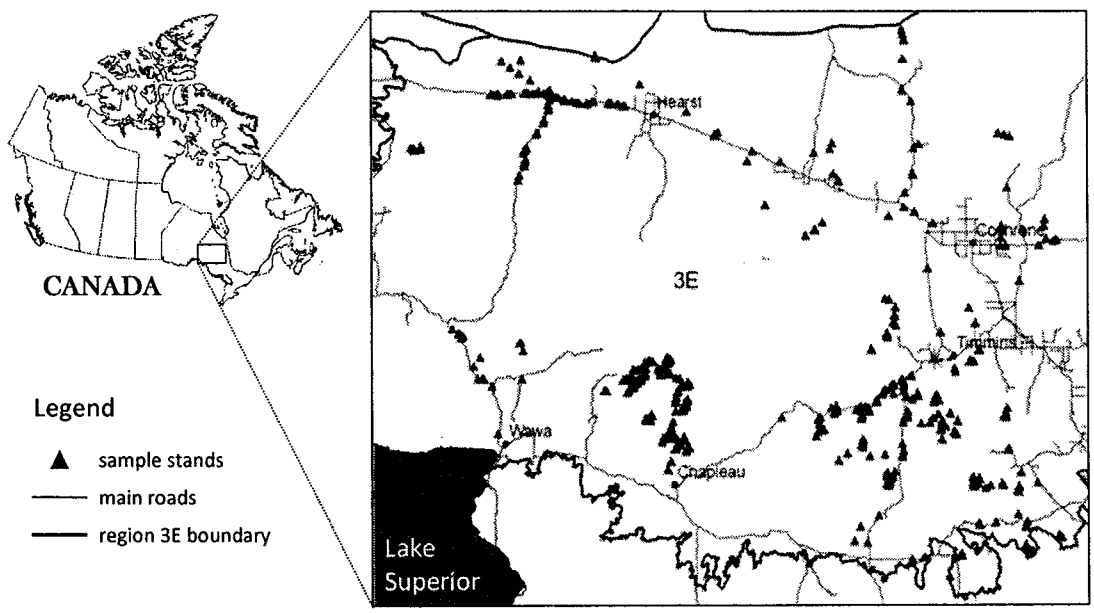

Figure 3.1 Map of the study area in region 3E in northeastern Ontario, Canada.

Sampling strategy

We sampled 361 stands across the study area. Sample stands were deliberately selected using stratified random sampling to capture a wide range of stand composition, age, and site conditions for fire-originated stands. We established our sampling frame from forest inventory plots that were ground surveyed in 1982 by the Ontario Ministry of Natural Resources (OMNR). To facilitate sampling, we stratified stands into: 1) species-dominant stands, defined as those stands dominated by ≥ 50% individual species; and 2) mixed-deciduous or coniferous stands, defined as those not considered species-dominant stand types, but dominated (≥ 50%) by either deciduous or coniferous basal area. We sampled a total of eight stand types: dominated by *P. banksiana* , *Populus* sp., *B. papyrifera* , *Picea* sp., *A. balsamea*, *T. occidentalis*, mixed deciduous, or mixed conifers (Table 3.1). For each stand type, we attempted to sample young (< 80 years), intermediate (80-120 years), and old (> 120 years) stands on both upland and lowland sites if applicable. Stands identified as barren and scattered or influenced by harvesting activities were not selected.

Each of the sample stands were then measured four to six times over 8-15 year intervals, encompassing a ~ 60 year time period, by combining ground survey measurements and sequential aerial photo interpretation measurements of each stand. Two measurements were from ground surveys, and two to four were from aerial photo interpretation. The ground survey measurements consisted of the original surveys conducted in 1982 by the OMNR and re-measurements of the same ground surveys completed by us between the years 2000 and 2003. Each ground survey consisted of a fixed 200 m long transect line, along which, 10 variable-radius point samples with a

wedge prism (basal area factor two) were established 20 m apart. At each point, live stems > 10 cm diameter at 1.3 m height were counted by species and considered as part of the tree canopy layer (Hayden et al., 1995). Three canopy stems of the dominant species, based on basal area, were selected. Heights and ages of these stems were measured and used to determine the site quality (Plonski, 1974). A soil pit was dug at the fifth point sample of each transect line. At each pit, soil characteristics were determined, including soil texture and moisture regime.

Aerial photo interpretation measurements were done using series of sequential aerial photos taken of the sample stands between 1946 and 1992 (provincial government records). Aerial photos older than 1986 were 1:15,840 scale, while more recent photography was 1:20,000. Photo interpretation was done by a qualified photogrammetry technician. To interpret the sample stands on the photos, the ground survey transect lines were located, as precisely as possible, on each sequential photo of the target area. A two hectare rectangular plot (100 x 200 m) was centered on the transect line and stand composition was interpreted within the plot following Zsilinszky (1963). Species basal areas, from photo interpretation, were calculated from % species cover, site quality (as determined from ground surveys), age (corrected from ground survey data to reflect year of photography) and estimated stocking (based on % canopy cover). Photo interpretation and species identification was verified from field checks on the re-measured ground surveys, taking note of what species dominated the snags and dead trees to confirm possible changes in composition through time. Less than four aerial photo measurements were conducted for some stands because the stands were either too young (< 20 years old) to be adequately interpreted in the earliest photos (Zsilinszky, 1963) or photos were

unavailable for particular target areas. We then combined the two ground surveys and the aerial photo interpretations for each stand plot to re-construct its developmental history, including changes in tree species composition and disturbance history (see Appendix I for an example).

Although both methods have been widely used in forest inventory operations (Husch et al., 2003), differences between aerial photo interpretation and ground surveys may confound observed transitions in stand composition between measurements. To determine the amount of difference, we randomly chose 30 stand plots where measurements of species composition were available from both aerial photo interpretation and ground surveys in 1982. Paired sample *t*-tests were used to determine if a significant difference could be detected. No significant difference in relative composition was found for *P. banksiana*, *Populus* sp., *B. papyrifera*, and *P. mariana*. However, that of *P. glauca* was underestimated by approximately 13%, while those of *T. occidentalis* and *A. balsamea* were overestimated by 4% and 10% in the aerial photos, respectively. When species were pooled into shade-intolerant and shade-tolerant groups, estimates between the two methods were not significantly different ($P > 0.05$).

Stand establishment date (i.e., time since fire, TSF) for stands < 80 years old was determined from Ontario fire history maps that documented fires > 200 ha between 1921 and 1978 (Donnelly and Harrington, 1978). For older stands, we used tree ages to estimate the date of the last fire (Bergeron, 1991). In the field, the same trees used to determine site quality were also used to determine TSF if they were clearly from the post-fire cohort. *P. banksiana*, *P. tremuloides*, *P. balsamifera*, *B. papyrifera*, and *P. mariana* were preferentially selected as they provide a more precise date of the last major

disturbance (Bergeron, 1991). Trees with fire scars that clearly survived fire(s) and were not part of the current age cohort were not sampled. In stands that were dominated only by shade-tolerant tree species such as *P. mariana*, *P. glauca*, *A. balsamea* or *T. occidentalis*, the least shade-tolerant tree species was chosen. When the more shade-tolerant trees were the oldest in a stand, and no fire scar(s) were found on the stems, we assumed that the less shade-tolerant trees were not a part of the initial cohort after fire. The more shade-tolerant trees were then used to determine TSF. Thus, TSF for stands dominated by shade-tolerant species is an approximation of minimum age of TSF. All increment cores were taken to the pith at breast-height (1.3 m above ground) and brought back to the laboratory. In the laboratory, the cores were mounted on constructed core strips and sanded to make rings visible. Rings were then counted using a hand-held magnifier until the same count was obtained three successive times. Time since fire was determined by adding 7 years to tree ages at breast height if the stand was dominated by *Populus* sp. or *B. papyrifera*, 8 years if dominated by *P. banksiana,* and 17 years if dominated by *P. mariana* or other shade-tolerant species based on an empirical model developed specifically for our study region (Vasiliauskas and Chen, 2002). Underestimation of TSF is possible when attaining tree age estimates from breast-height measurements, particularly for shade-tolerant species (Gutsell and Johnson, 2002; Parent et al., 2002). When possible, we avoided using *A. balsamea* for estimating TSF (Kneeshaw and Claveau, 2001).

Response and predictor variables

The response variable was prepared by classifying the observed stand plots at each measurement into one of eight discrete stand types (Table 3.1) based on the relative

percentage of species basal area present and using the stand classification scheme described above for sampling. Plot measurements dominated equally by two or more species were classified based on the most shade-tolerant species (Humbert et al., 2007). Order of species with increasing shade-tolerance and their corresponding stand type abbreviations are as follows: *P. banksiana* < *Populus* sp. < *B. papyrifera* < *Picea* sp. < *A. balsamea* < *T. occidentalis*. *Populus* sp. includes stands dominated by *P. tremuloides* or *P. balsamifera* (> 95% were dominated by *P. tremuloides* based on field cruised data). *Picea* sp. includes stands dominated by *P. mariana* or *P. glauca* (> 80% were dominated by *P. mariana*). These groupings were made due to difficulty in discriminating these species on the small scale aerial photography (Zsilinszky, 1963).

Table 3.1 Summary statistics for each initial stand type group.

Initial stand types [a]		Sample size [b]	TSF distribution [c]	Successive stand types observed
1.	*Pb*	214	63 (20, 138)	*Pb*, *Pm*, *MC*
2.	*Pt*	248	81 (22, 241)	*Pt*, *Pm-Ab* [d], *MC*, *MD*
3.	*Bp*	157	121 (21, 273)	*Bp*, *Pm-Ab* [d], *MC*, *MD*
4.	*Pm*	420	133 (26, 268)	*Pm*, *To*, *MC*
5.	*Ab*	78	151 (42, 367)	*Ab*, *Bp*, *Pm*, *MC*
6.	*To*	118	203 (79, 390)	*To*, *MC*
7.	*MD*	58	110 (27, 230)	*MD*, *Pm-Ab* [d], *MC*
8.	*MC*	236	138 (21, 383)	*MC*, BW, *Pm-Ab* [d], *To*, *MD*

[a] Discrete stand types abbreviations: *Pb* = *P. banksiana* dominated, *Pt* = *Populus* sp. dominated, *Bp* = *B. papyrifera* dominated, *Pm* = *Picea* sp. dominated, *Ab* = *A. balsamea* dominated, *To* = *T. occidentalis* dominated, *MD* = mixed deciduous dominated, and *MC* = mixed coniferous dominated.
[b] Sample size refers to the number of transitions observed for each initial stand type group.
[c] Number outside bracket is mean TSF of sample stands in each initial stand type group. Numbers inside bracket are the observed min. and max. TSF.
[d] Merged category of *Pm* and *Ab* dominated stand types.

Less than two percent of our plot measurements included cases where stands were dominated equally by two or more species. Because we classified these measurements by

the most shade-tolerant species an inherent methodological bias is potentially introduced. To test for bias, we also conducted a separate analysis in which the plot measurements were classified by the less shade-tolerant species. Both methods of classifying plot measurements yielded the same overall model results.

Predictor variables selected for analysis included: TSF, land class (LC), and intermediate disturbances (DIS) (Table 3.2). Land class was used as a proxy for edaphic conditions, derived from soil texture and moisture measurements at each ground survey. We assumed that LC did not change for a period of 60 years. Land class was summarized into two broad categories: 1) LC1, characterized by fine to medium textured soils and moist to wet soil moisture conditions; and 2) LC 2, characterized by medium to coarse textured soils and fresh to dry soil moisture conditions.

Intermediate disturbances (DIS) were those where up to 75% of the canopy trees were destroyed. Stands with > 75% destruction, which were considered stand replacing, were excluded from our study. The DIS variable was summarized into two broad categories indicating the 'presence' or 'absence' of disturbance between two consecutive measurements. Measurements on each plot were investigated for evidence of windthrow damage and insect infestation from SBW and FTC since the last measurement. Insect damage data was acquired from insect infestation maps produced annually for Ontario by the Forest Insect and Disease Survey conducted by the Canadian Forest Service since 1941. Insect damage was considered 'present' if there was evidence of approximately three years of infestation since the last measurement. Spruce budworm damage was the most prevalent form of disturbance, with the last major outbreak in the region occurring between 1972 and 1981. Ninety and 64% of all disturbance damage in *A. balsamea* and

mixed conifer stands, respectively, were caused by SBW infestation. Windthrow damage was assessed from aerial photographs and ground survey inspection. Windthrow damage was considered present if between 10 and 75% of the trees in the stand were uprooted or broken off. Several plots showed evidence of minor fire damage, but were excluded from our analysis.

Table 3.2. Predictor variables used in analyzing stand type transitions.

	Variable	Abbreviation	Type	Units	Proxy for
1.	Time since fire	TSF	Continuous	Years	Stand age
2.	Land class	LC	Categorical	LC 1, LC 2	Soil type and moisture conditions
3.	Intermediate disturbance	DIS	Categorical	Absence, Presence	Disturbance from windthrow, spruce budworm, and forest tent caterpillar

Data analysis

In order to determine whether successional pathways were predictable from TSF, LC, and DIS between two consecutive measurements for each stand plot, stand measurements were grouped based on their preceding stand type (Table 1 and Appendix I). Since repeated measurements were conducted on each stand plot, there is potential violation of the assumption of independence among observations. Although the sequence of measurements on each stand plot spans a ~ 60 year time period, they were not analyzed longitudinally because each initial stand type group was modeled separately. Potential correlation between measurements on stand plots was negligible since individual measurements were partitioned during the initial stand type grouping process (Appendix I).

For each stand type group, we used multinomial logistic regression to test if probability of stand transition was significantly related to TSF, LC, and DIS. The preceding stand type was used as the baseline category for the logits in each multinomial regression model. Some of the successive stand types observed for each preceding stand type had too few observations to correctly perform the multinomial regressions. In these cases, successive stand types that made-up less than 5% of the total observations in each group were critically re-examined. When two or more successive stand types were each less than 5%, but relatively similar in life history characteristics, they were merged and re-classified as a new combined successive stand type. Such was carried out for successive *Pm* and *Ab* stand types observed in several groups (Table 3.1). If the successive stand type had too few observations and could not be re-classified or merged, we then deemed it an outlier and discarded.

For each multinomial regression, we fitted a saturated model (main effects variables and interactions) using the R statistical language and environment (version. 2.8.1; R Development Core Team 2008). Backwards elimination using the Wald Statistic was used for variable exclusion (Kutner et al., 2005). A critical value of $\alpha = 0.1$ was used to explore those variables having a marginal effect on individual multinomial logits (Appendix II). The overall significance of the variables retained in each model was also assessed using the Likelihood Ratio Test for individual parameters (Table 3.3). However, one of the ambiguities in assessing predictor variables in multinomial regression is that predictors may be siginificant for individual logits, based on the Wald Statistic, yet simultaneously non-significant for the overall model based on the Likelihood Ratio Test. In such situations, variable retention is up to the modeler's discretion (Kleinbaum and

Klein, 2005). This was the case for the LC variable in the *MC* stand type model. Land class was non-significant overall (Table 3.3), but it was significantly related to the transition to *To* stand type ($P < 0.05$; Appendix II) and thus was retained. Overall model significance and goodness-of-fit was judged using the Likelihood Ratio Statistic and assessing change in Akaike's Information Criterion (AIC) scores between the null (intercept only) and final models (Kutner et al., 2005) (Table 3.3). A change in AIC of > 2 is considered a substantial change in the descriptive ability of the final model over the null (Chatterjee and Hadi, 2006).

3.3 Results

Shade-intolerant, species-dominant stand types

Stand transition of shade-intolerant stand types (i.e., *Pb*, *Pt*, and *Bp*) was highly related to TSF ($P < 0.01$; Table 3.3). With increasing TSF, *Pb*, *Pt*, and *Bp* stand types were less likely to remain the same composition and demonstrated multiple successional pathways towards mixed-species stands or stands dominated by shade-tolerant species (Figs. 3.2a, b, c, and d). The probability of *Pb* stands remaining the same decreased substantially with TSF. By year 138, the probability of *Pb* stands remaining dominated by *P. banksiana* had decreased to less than 50%, significantly lower than that observed for *Pt* and *Bp* stands of similar age (Figs. 3.2c and d). Model predictions indicated that *Pt* and *Bp* stand types would persist longer on the landscape, showing a > 50% probability of dominance 200 years after fire (Figs. 3.2c and d).

Table 3.3 Significance test and predictor variables retained for each multinomial regression model.

Model		*K*	*G*	*Δ*AIC	Variable [a]
1.	*Pb*	4	34.7**	26.7	TSF**
					LC**
2.	*Pt*	3	18**	11.9	TSF**
3.	*Bp*	3	20.2**	14.3	TSF**
4.	*Pm*	4	21.8**	13.8	TSF**
					LC**
5.	*Ab*	3	32.6**	26.6	DIS**
6.	*To*	1	4.5*	2.5	LC*
7.	*MD*	2	6.4*	2.4	TSF*
8.	*MC*	12	36.9**	12.9	TSF*
					LC^{ns}
					DIS**

Notes: Abbreviations are: *k*, the number of parameters estimated in the model; *G*, the likelihood ratio statistic from maximum-likelihood estimation; *Δ*AIC, the increase of AIC when final model is compared with null model.

[a] Likelihood Ratio test for individual variables was used to judge overall significance in model. Appendix II summarizes individual parameter estimates of variables for each logit in each model.
[ns] not significant; * $P < 0.05$; ** $P < 0.01$.

Change in the *Pb* stand type was also affected by LC ($P < 0.01$; Table 3.3). *Pb* stands were less likely to continue to dominate on moist, finer textured soils (i.e., LC 1) and transitioned to *MC* or *Pm* stand types earlier compared to LC 2 sites (Figs. 3.2a and b). However, transition of *Pt* and *Bp* stand types was not significantly related to LC (Table 3.3). While both *Pt* and *Bp* groups showed the same successive stand type categories over time, transition to *MD* stands in the *Bp* group was not significantly related to TSF (Fig 3.2d) (Appendix II). Furthermore, transition of the three shade-tolerant stand types was not affected by DIS (Table 3.3).

The order of probability estimates for the successive stand types observed in each of the shade-intolerant models followed a gradient with increasing shade-tolerant species component over time. In Fig. 3.2c, as the probability of *Pt* stands remaining the same diminishes, the most probable stand replacement is *MD*, then *MC*, followed by *Pm-Ab* stand types. Re-examination of the successive *MC* stands observed for the shade-intolerant stand types revealed that ~ 30% were dominated by either *Picea* sp. or *A. balsamea*. Thus, the observed sequences of probability estimates appear to demonstrate a progressive replacement of the post-fire cohort by *Picea* sp. and *A. balsamea*. It should be noted however, that *Picea* sp. was sometimes underestimated in the aerial photo measurements, while *A. balsamea* was overestimated (see Materials and Methods section).

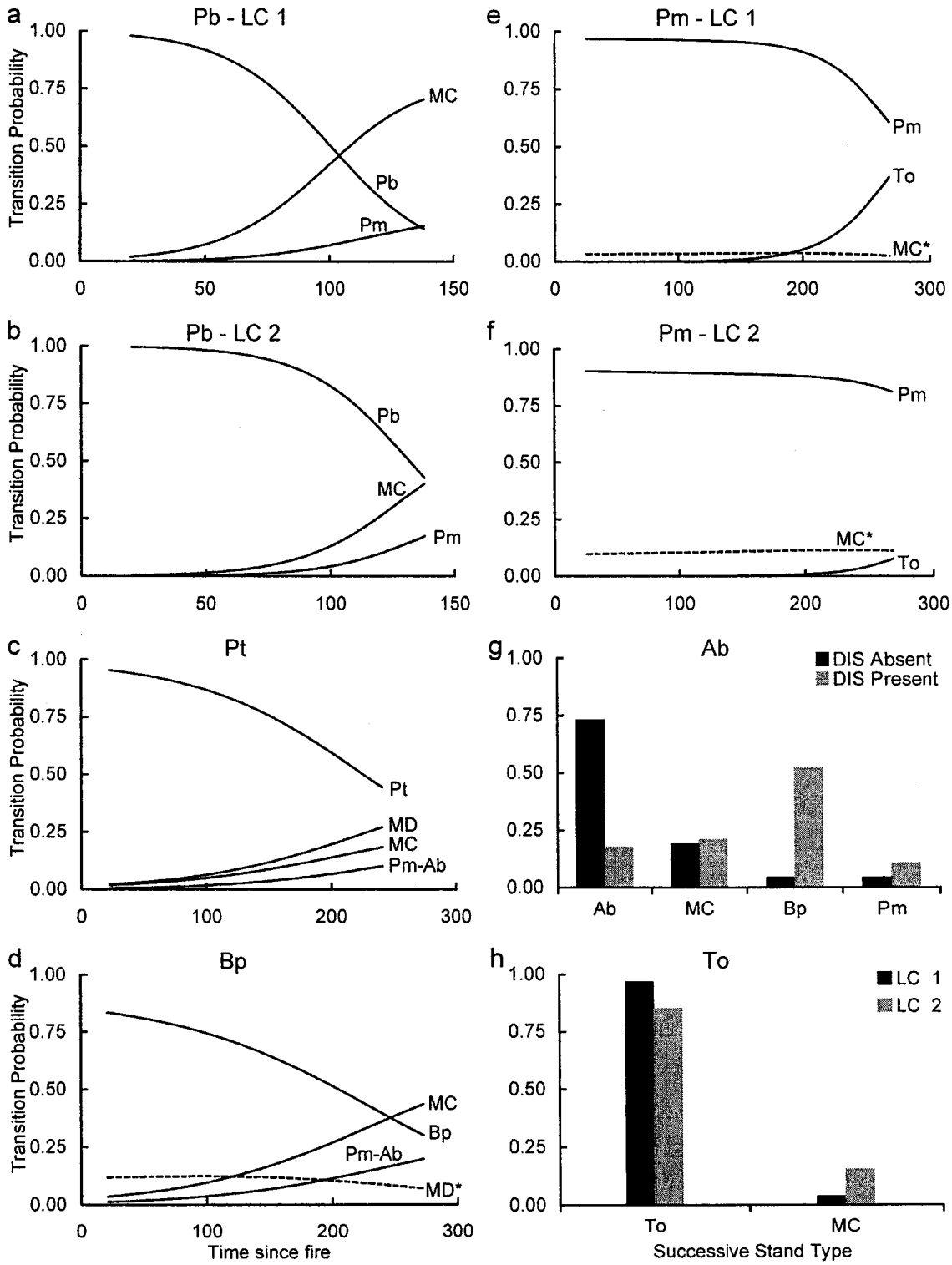

Figure 3.2 The predicted transition probabilities as a function of time since fire (TSF, years) for: a) *P. banksiana* dominated *Pb* stands on moist to wet land class (LC 1) sites; b) *Pb* stands on fresh to dry land class (LC 2) sites; c) *Populus* sp. dominated *Pt* stands; d) *B. papyrifera* dominated *Bp* stands; e) *Picea* sp. dominated *Pm* stands on LC 1 sites; f) *Pm* stands on LC 2 sites; g) *A. balsamea* dominated *Ab* stands as a function of the

absence or presence of intermediate disturbance (DIS); and h) *T. occidentalis* dominated *To* stands as a function of LC. Note: * and dashed trend lines indicate transition probability is not significantly (P > 0.05) related to TSF.

Shade-tolerant, species-dominant stand types

Models for the shade-tolerant stand types were more variable concerning the predictor variables retained and the successive stand types observed compared with those of the shade-intolerant types (Figs. 3.2e, f, g, and h). Transition of *Pm* stand type significantly related to TSF and LC (Table 3.3). However, *Pm* stands remained relatively stable throughout time (Figs. 3.2e and f); particularly on moist and wet sites (i.e., LC 1) where the probability of *Pm* stand dominance was still > 90% approximately 200 years after fire (Fig. 3.2e).

Transition in *Ab* and *To* stands was not related to TSF (Table 3.3). Both groups exhibited a strong tendency to remain the same composition over time (Figs. 3.2g and h). Transition in *Ab* stands, however, was related to DIS (P < 0.01; Table 3.3). When disturbed, *Ab* stands were likely to change to *Bp* stands or, to a lesser extent, *MC* stands (Fig. 3.2g). *To* stands demonstrated the strongest tendency to remain the same composition over time. Although *To* stands did show a small (~ 15%) probability of transitioning to *MC* stands on LC 2 sites (P < 0.05; Table 3.3) (Fig. 3.2h), they showed a > 95% probability of remaining the same on LC 1 sites (Fig. 3.2h).

Mixed deciduous and coniferous stand types

MD stands displayed similar succession patterns as the *Pt* and *Bp* stand types, but showed a greater probability of transitioning to *MC* stands as TSF increased (P < 0.05; Table 3.3) (Fig. 3.3a). Persistence of *MD* stands remained approximately 50% 240 years after fire, slightly higher than *Pt* and *Bp* stands. Transition to *Pm-Ab* stands was unrelated

to any of the predictor variables (Appendix II). This should be interpreted cautiously since *MD* stands had the smallest sample size (Table 3.1).

MC stands had the highest number of successive stand type categories observed and most predictor variables retained (Tables 3.1 and 3.3). This can be expected since the *MC* classification scheme included any mixture of coniferous species, sometimes differing greatly in life history traits, e.g., *P. banksiana* and *T. occidentalis*. Nonetheless, amongst the variability several significant trends were observed. Transition of *MC* stands to *Bp* and *MD* stands was positively related to the presence of DIS ($P < 0.05$ and $P < 0.01$, respectively; Appendix II) (Figs. 3.3b and d). Although transition of *MC* stands to *Pm-Ab* stands was only marginally related to TSF ($P < 0.1$), transition to *To* stands was significantly related to TSF ($P < 0.01$; Appendix II). Transition to *To* stands was also related to LC, with *T. occidentalis* most likely to become dominant on LC 1 sites (Figs. 3.3b and c). The presence of DIS was also marginally related to transition to *To* stands ($P < 0.1$; Appendix II) and was caused mainly by SBW outbreak.

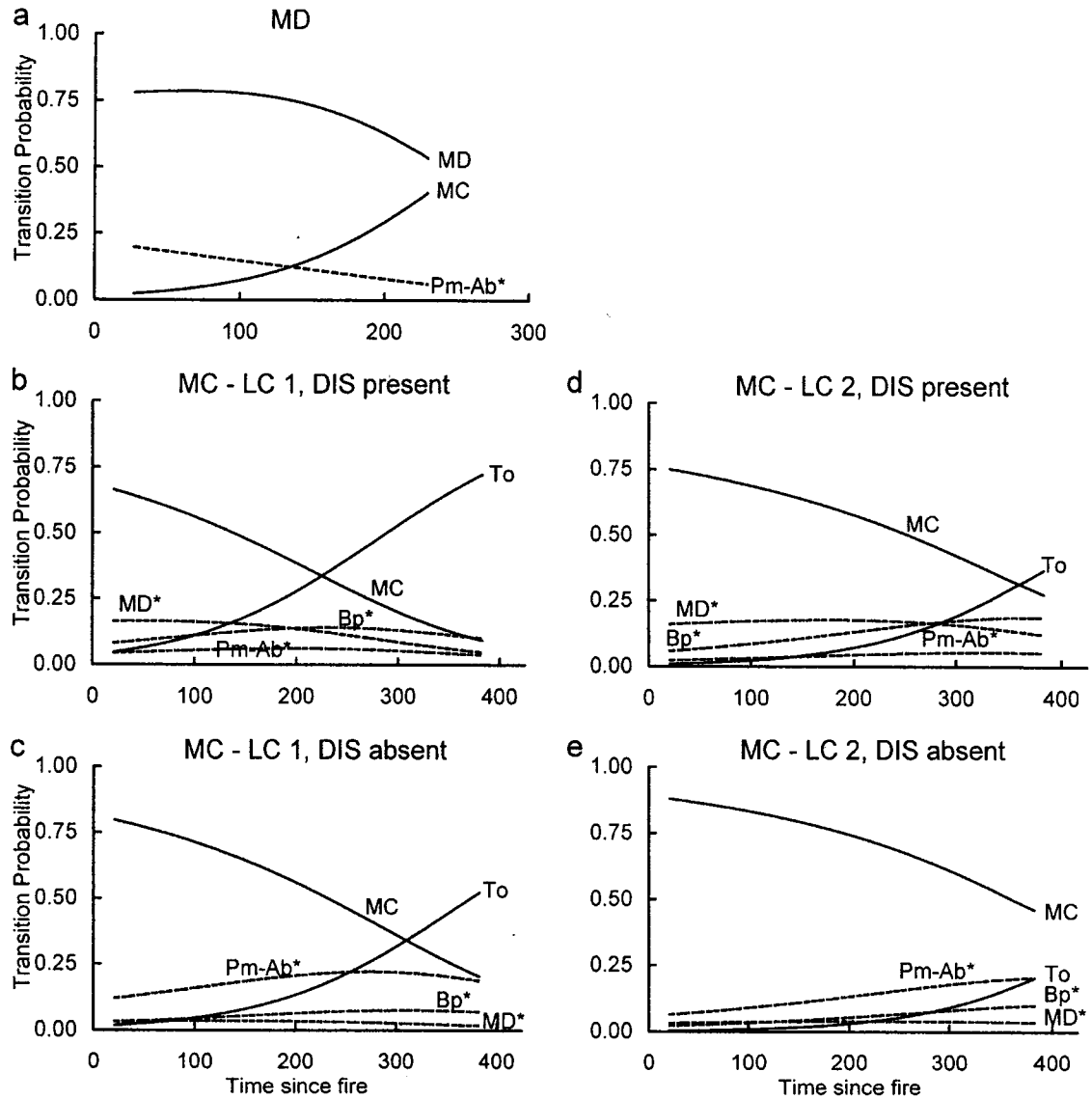

Figure 3.3 The predicted transition probabilities as a function of TSF for: a) mixed deciduous (*MD*) stands; b) mixed coniferous (*MC*) stands on moist to wet land class (LC 1) sites with intermediate disturbance (DIS) present; c) *MC* stands on LC 1 sites with DIS absent; d) *MC* stands on fresh to dry land class (LC 2) sites with DIS present; and e) *MC* stands on LC 2 sites with DIS absent. Note: * and dashed trend lines indicate transition probability is not related to TSF.

3.4 DISCUSSION

Effects of TSF on successional pathways

In the prolonged absence of stand-replacing fire, we observed stands of similar initial species composition demonstrate multiple successional pathways. Pathways of stands dominated by shade-intolerant species were mostly related to TSF, demonstrating an overall increase in probability of transitioning to stands dominated by shade-tolerant species with increasing TSF. Conversely, pathways of stands dominated by shade-tolerant species were less dependent on TSF and tended to remain the same composition overtime, or transitioned to stands still dominated by shade-tolerant species – unless disrupted by intermediate disturbances. These observations are congruent with previous boreal forest studies that report post-fire stands dominated by fast growing shade-intolerant species are eventually replaced by shade-tolerant species in the long-term absence of disturbance (Carleton and Maycock, 1978; Bergeron and Dubuc, 1989; Frelich and Reich, 1995; Bergeron, 2000). We believe the relationship with TSF can be explained by 'neighborhood effects' (Frelich and Reich, 1995; Frelich and Reich, 1999) that operate over the course of stand development, specifically, overstory tree species responses to modification of the understory light environment, forest floor properties and competition from nearby seed sources.

Light variation in the understory during stand development is considered a key mechanism affecting understory species establishment and compositional direction in boreal ecosystems (Frelich and Reich, 1995; Bergeron, 2000). We observed a clear shift in *P. banksiana* dominated stands towards mixed-conifer and *Picea* sp. stand types within 150 years after fire. Under natural conditions, *P. banksiana* does not reproduce

vegetatively and is one of the least shade-tolerant tree species in its native range (Burns and Honkala, 1990; Humbert et al., 2007). Re-establishment of *P. banksiana* in the shade of its own canopy is unlikely and it is usually displaced by more shade-tolerant species (Gauthier et al., 1993; Frelich and Reich, 1995). Similarly, stands of shade-intolerant *Populus* sp. and *B. papyrifera* also decreased over time, but not to the extent observed for *P. banksiana*. *Populus* sp. and *B. papyrifera* are more shade-tolerant than *P. banksiana* and can reproduce vegetatively through root and stump sprouting (Burns and Honkala, 1990; Humbert et al., 2007). Their ability to re-invade gaps created by the senescence of post-fire cohort trees by seeding and sprouting may permit self-replacement (Kneeshaw and Bergeron, 1998; Cumming et al., 2000) and as our results suggest allows some deciduous stands to remain dominant for longer periods of time. It appears that re-establishment of *Populus* sp. and *B. papyrifera* under their own canopy is also dependent on neighborhood effects, including changes in forest floor organic matter thickness over time, and competition for gap resources by more shade-tolerant species (Lavertu et al., 1994; Kneeshaw and Bergeron, 1998; Fenton et al., 2005). Increases in litter and humus layer thickness with TSF have been shown to have an inhibitory effect on seed germination in *Populus* sp. and *B. papyrifera* and sprouting production of *P. tremuloides* (Lavertu et al., 1994; Greene et al., 1999). Conversely, increases in moss cover and rotten logs with increasing TSF, along with break-up of the post-fire overstory, can favor the recruitment of shade-tolerant conifers (Simard et al., 1998; Peters et al., 2006). Still, this is ultimately dependent on the proximity of seed sources, which can limit colonization and competition in the understory (Tilman, 1994; Turner et al., 1998). Nonetheless, assuming the presence of shade-tolerant species at the stand's edge, it will take longer for

their regeneration to reach the center of large stands relative to smaller ones. Further, the dispersal of shade-tolerant species may also be obstructed by local physiographic conditions (e.g., water bodies and landforms) which can alter the timing and direction of succession in deciduous stands (Albani et al., 2005).

Effects of edaphic conditions on successional pathways

Local edaphic conditions can influence the course of succession since the recruitment and performance of species during post-fire colonization is directly dependent on the type and availability of soil substrate (Robichaud and Methven, 1993; Simard et al., 1998; Lecomte and Bergeron, 2005). Although *P. banksiana* stands succeeded to mixed-conifer and *Picea* sp. stands as TSF increased, succession was delayed on dryer, coarser textured soils (i.e., LC 2 sites). Similarly, Gauthier et al. (1993) noted that *P. banksiana* may dominate for longer periods on poorer, dryer sites, but give way to *Picea* sp.–*A. balsamea* associations sooner on richer soils. We suspect this divergence is related to differential species recruitment and development on post-fire sites. Provided an adequate seed source, *P. banksiana* is more likely to successfully regenerate and grow on dry, sandy or gravelly soils relative to *Populus* sp., *B. papyrifera*, or *Picea* sp. (Burns and Honkala, 1990; Lecomte and Bergeron, 2005). Stands with higher initial *P. banksiana* density may dominate for longer time periods since there is less pressure from competing tree species for stand resources. In addition, lower crown densities typically found on xeric sites may actually facilitate some self-replacement of *P. banksiana* since natural openings provide enough light in the understory for recruitment (Gauthier et al., 1993). Also, scarce resource availability (typical of excessively dry or wet soils – further discussed below for *Picea* sp. and *T. occidentalis*) can increase tree

longevity, which may contribute to their prolonged dominance on resource limited sites (Robichaud and Methven, 1993).

Picea sp. and *T. occidentalis* dominated stands showed the highest probability of remaining the same composition over time, with the exception of *Picea* sp. stands shifting to *T. occidentalis* on lowland (i.e., LC 1) sites, approximately 200 years after fire. This may be misleading however, since edaphic conditions within the LC 1 category range from wet organic deposits to moist, fine textured soils. Fifty eight percent of *Picea* sp. stands sampled on LC 1 sites comprised of wet organic deposits dominated by *P. mariana*. These forest types are known to be compositionally stable communities and are most likely to remain dominated by *P. mariana* over time (Lecomte and Bergeron, 2005). Indeed, re-examination of our data showed that 98% of *Picea* sp. stands sampled on wet organic deposits remained dominated by *P. mariana* at the next measurement. Transition to *T. occidentalis* stand types occurred mainly on plots characterized by moist, fine textured soils. Therefore, replacement of *P. mariana* by *T. occidentalis* is plausible on mesic sites, but is unlikely on lowland areas already dominated by *P. mariana*.

The small, yet increased, probability of *Picea* sp. and *T. occidentalis* stands shifting to mixed-conifer stands on upland (i.e., LC 2) sites and the reverse trend occurring on lowland (i.e., LC 1) sites may be related to niche differentiation and species competitive ability on resource limited soils as described by the resource-ratio hypothesis of plant succession (Tilman, 1985; Tilman, 1994). *Picea* sp. and *T. occidentalis* stands sampled on LC 1 sites consisted largely of organic deposits with moist to wet soil conditions. Decomposition rates are naturally low and nitrogen availability is limited (Fenton et al., 2005; Simard et al., 2009). The resource-ratio hypothesis predicts that the

best competitor for a single limiting resource should displace all other species. Correspondingly, *P. mariana* and *T. occidentalis* have a high tolerance to increased soil moisture and low nutrient availability relative to other boreal tree species (Burns and Honkala, 1990; Wang et al., 2003). Their tolerance to shade and ability to regenerate by seeding and vegetative layering under a conspecific canopy allows them to progressively re-invade and survive in the understory, and permits their dominance on LC 1 sites (Lecomte and Bergeron, 2005). Alternatively, well-drained, productive soils, characteristic to upland, mesic sites, are less inhospitable and can provide greater opportunity for the recruitment and colonization of less competitive species or species of different niches. This also supports the hypothesized positive relationship between species diversity and productivity driven by environmental conditions across sites (Loreau et al., 2001).

Effects of intermediate disturbances on successional pathways

Intermediate disturbances disrupt the gradual internal workings of the ecosystem and accelerate, slow or redirect the course of succession by 'selectively weeding' certain species from the overstory and creating new growing space for recruitment (Kneeshaw and Bergeron, 1998; Bouchard et al., 2006; Rich et al., 2007). Because we did not differentiate between types of intermediate disturbances in our analysis, our interpretation of intermediate disturbance effects is based on its species-specific association (i.e., spruce budworm and forest tent caterpillar) or its effects on types of species coupled with site conditions.

Forest tent caterpillar infestation is an important disturbance affecting *Populus* sp. and *B. papyrifera*, and is considered to accelerate succession from deciduous to

coniferous dominance in boreal forest (Chen and Popadiouk, 2002); however, no relationship was detected. The effects of forest tent caterpillar on *Populus* sp. growth and mortality have been well documented, but little quantitative information has been published regarding its influence on succession (Cumming et al., 2000). Increased light levels in the understory caused by forest tent caterpillar defoliation is considered to promote competing shrub and conifer regeneration; however, in areas adjacent to our study Man et al., (unpublished data, R. Man, T. Scarr and J.A. Rice) report that after forest tent caterpillar outbreaks, *P. tremuloides* regeneration is often sufficient to compete with developing shrubs and shade-tolerant conifers. This self-replacement process may explain the insignificant effect we observed.

Spruce budworm infestation facilitates the maintenance of shade-intolerant deciduous species in mature boreal forest (Kneeshaw and Bergeron, 1998). In our results, *A. balsamea* and mixed-conifer stand types showed an increased probability of transitioning to deciduous dominated stand types when severally impacted by spruce budworm outbreak. Gaps created in the overstory from spruce budworm induced tree mortality can increase light levels on the forest floor and potentially promote *Populus* sp. and *B. papyrifera* regeneration. This may have contributed to the observed persistence of *Populus* sp. and *B. papyrifera* dominated stands in our results. However, the degree to which these species will establish may vary, depending on: 1) the relative abundance of deciduous species present before infestation, 2) edaphic conditions, and 3) the duration and severity of spruce budworm outbreak (Kneeshaw and Bergeron, 1998; Bouchard et al., 2006). Bouchard et al., (2006) observed that upper slope stands dominated by *A. balsamea* were more likely to change to deciduous composition after severe spruce

budworm infestation compared with lower slope stands where a cyclic reoccurrence of *A. balsamea* is common, largely because lower slopes are cooler and less well drained, thus less favourable for deciduous species recruitment relative to *A. balsamea* (Bouchard et al., 2006). Nonetheless, even under suitable post-outbreak conditions for deciduous establishment, these stands eventually progress towards shade-tolerant conifer dominance over time (Kneeshaw and Bergeron, 1998). Severe outbreaks may destroy mature *A. balsamea* trees, but young regeneration is less likely to be effected (MacLean, 1980). *A. balsamea* are known to form extensive seedling banks under their own canopy. Provided adequate propagules for re-establishment *A. balsamea*, *Picea* sp., and *T. occidentalis* progressively recruit in the understory, including in gaps too small to foster *B. papyrifera* and *Populus* sp. regeneration (Kneeshaw and Bergeron, 1998). In old coniferous stands severely affected by spruce budworm outbreak, *T. occidentalis* may even out-compete *A. balsamea* and *Picea* sp. (Kneeshaw and Bergeron, 1998; Bergeron, 2000). This is reflected in our results, in the mixed-conifer stand type, where disturbance led to an increased probability of succeeding to *T. occidentalis* dominance.

Intermediate wind disturbance is reported to have varying effects on the course of succession in boreal forest, largely depending on stand age, understory composition and site conditions (Webb, 1988; Rich et al., 2007; Ilisson et al., 2007). In pioneer stands dominated by shade-intolerant species, wind may accelerate succession by toppling post-fire overstory trees and releasing shade-tolerant conifers when present (Abrams and Scott, 1989; Rich et al., 2007). Shade-intolerant *P. banksiana*, *Populus* sp. and *B. papyrifera* typically allocate more resources to rapid growth than structural strength compared with shade-tolerant conifers, making them susceptible to wind damage,

particularly stem breakage (Burns and Honkala, 1990; Rich et al., 2007). Nonetheless, no wind effect was detected in our shade-intolerant species stands. Rather, intermediate disturbance effects were only observed in *A. balsamea* and mixed-conifer stands, which tended to revert to deciduous dominance once disturbed. While this conflicts with the 'accelerated succession' hypothesis above, it does agree with many previous reports that mature *P. mariana*, *P. glauca* and *A. balsamea* are very susceptible to wind damage due to their shallow rooting habit and dense foliage, particularly on wet, shallow soils (Burns and Honkala, 1990; Steil et al., 2009). We suspect that wind may accelerate succession in mature, post-fire stands of shade-intolerant species when shade-tolerant regeneration is present, but, similar to spruce budworm disturbance, may in fact slow succession in old shade-tolerant conifer stands that still contain sufficient numbers of deciduous trees to compete for gap space. This may be especially true for wind disturbed sites since shade-tolerant conifers tend to up-root rather than break-off when blown-over, therefore increasing the area of mineral soil exposed in the stand which can promote deciduous germination, particularly if disturbance is followed by a mast year (Greene et al., 1999; Ilisson et al., 2007).

Convergence to shade-tolerant species

Despite the multiple pathways of succession we observed, our results also seem to suggest an overall 'convergence' pattern towards relatively constant species composition dominated primarily by shade-tolerant species. This convergence is demonstrated, firstly, by the increased probability of *P. banksiana*, *Populus* sp. and *B. papyrifera* stands to transition to stands dominated by *A. balsamea*, *Picea* sp. and *T. occidentalis* over time; and secondly, the high probability of stands dominated by shade-tolerant species,

including mixed-conifer stands, to remain dominated by shade-tolerant species. This was especially true for *T. occidentalis* dominated stands, which showed the greatest tendency to remain the same composition over time. Similar observations were made by Grigal and Ohmann (1975) and Bergeron and Dubuc (1989), who suggested *T. occidentalis* as the likely climax species in areas were seed sources are abundant, i.e., shore lines and lowlands.

Although contemporary research stresses that complete convergence is unlikely because site-dictated factors (e.g., physiography, edaphic conditions), species dispersal, and disturbances will undoubtedly lead to differences among late succession associations (Christensen and Peet, 1984; Woods, 2007), the observed convergence pattern does agree with previous studies who have made similar observations in adjacent boreal forests (Grigal and Ohmann, 1975; Bergeron and Dubuc, 1989; Frelich and Reich, 1995).

3.4 CONCLUSION

Using a set of long-term repeated measurements, covering a range of stand types over a wide geographical area, our results showed that in the prolonged absence of stand-replacing fire, compositionally similar stands underwent multiple successional pathways, depending on TSF, edaphic conditions and intermediate disturbances. Pathways of stands dominated by shade-intolerant species were most related to TSF and showed an increase in probability of transitioning to stands dominated by shade-tolerant species. This relationship seemed largely explained by neighborhood effects, including modification of the understory light environment and increases in forest floor organic matter over time. Pathways of stands already dominated by shade-tolerant species appeared less affected by TSF and more dependent on edaphic conditions and disturbances.

Differing edaphic conditions produced divergent pathways in stands of similar initial composition by affecting resource availability, which influenced what species established and their performance over time. Very dry, coarse textured soils or water saturated, nutrient poor soils, favored the best competitor species, capable of tolerating limited resources, as predicted by the resource-ratio hypothesis. On resource limited sites the most competitive species remained dominant for longer periods compared to sites where resources were abundant and competitive niche was less important. Conversely, richer soils permitted invasion and promoted species mixtures during succession, corroborating the general hypothesis of species diversity as a function of site productivity.

Intermediate disturbances affected successional direction by reducing overstory competition and promoting recruitment in the understory. Although some disturbances

are considered to accelerate succession (i.e., forest tent caterpillar and windthrow), no evidence was detected. Rather, disturbance effects were detected in *A. balsamea* and mixed-conifer stands (e.g., spruce budworm and windthrow) and tended to promote deciduous persistence and species diversity in old growth forest. Nonetheless, if undisturbed by stand-replacing agents, we suspect boreal stands will eventually converge towards stands dominated by shade-tolerant species. This phenomenon appears largely facilitated by the ability of shade-tolerant species to progressively recruit and grow in the understory.

CHAPTER FOUR: TESTING THE POPULATION DYNAMICS OF BOREAL TREE SPECIES USING LONG-TERM REPEATED MEASUREMENTS OF STAND DEVELOPMENT

4.1 INTRODUCTION

Vegetation succession is commonly viewed as a community-level phenomenon, expressed through temporal changes in the populations of plant species which comprise the community. In North America's boreal forest, secondary succession is largely controlled by forest fire frequency. In many areas, particularly in north western North America, the average time between stand-replacing fire is shorter than the life span of the dominant tree species (<150 years) (Larsen, 1997; Weir et al., 2000). In these areas, temporal changes in tree species composition are often limited (Gutsell and Johnson, 2002; Chen et al., 2009; Ilisson and Chen, 2009). More commonly observed on the landscape is a cyclic reoccurrence of fire adapted species, e.g., *Pinus banksiana* (Ait.), *Populus tremuloides* (Michx.) and *Picea mariana* (Mill.) (Gauthier et al., 1993; Johnstone and Chapin, 2006).

In central and eastern regions of North America's boreal forest, secondary successional processes are more apparent as the average fire cycle is longer (Wein and Moore, 1979; Lauzon et al., 2007). This process has been described as a shift in species abundance from post-fire stands dominated by shade-intolerant, pioneer species to replacement by late seral, shade-tolerant shrub and tree species, including *Corylus cornuta* (Marsh.), *Acer spicatum* (Lamb.), *Picea glauca* (Moench) Voss., *Abies balsamea* (L.) Mill., and *Thuja occidentalis* (L.) (Carleton and Maycock, 1978; Bergeron and Dubuc, 1989).

Although the simple species-replacement model of shade-intolerant by shade-tolerant species over time is commonly acknowledged, contemporary studies increasing reveal the complexity of long-term vegetation dynamics in boreal ecosystems (Chen and Popadiouk, 2002; Johnson and Miyanishi, 2008). Species recruitment and colonization are often limited by physical site conditions (e.g., edaphic conditions), intermediate disturbances and species interaction effects (e.g., competition and facilitation) (Tilman, 1994; Frelich and Reich, 1995; Ilisson and Chen, 2009). Shade-intolerant species, commonly considered to diminish in the prolonged absence of stand-replacing fire, may form subsequent cohorts under suitable conditions. *P. banksiana* is more likely to colonize dry, sandy or gravelly soils relative to other boreal species (Rudolph and Laidly, 1990; Lecomte and Bergeron, 2005). Naturally low canopy closure on xeric sites and low competition from invading species, may permit self-maintenance of *P. banksiana* (Gauthier et al., 1993). Provided sufficient gap size and low competition from more shade-tolerant species, *P. tremuloides* and *B. papyrifera* may form self-perpetuating cohorts (Pare and Bergeron, 1995; Kneeshaw and Bergeron, 1998; Cumming et al., 2000). *A. balsamea* are commonly considered to form self-perpetuating climaxes due to their shade-tolerance and production of extensive seedling banks; however, on upland sites, when severely infested by spruce budworm, stands of *A. balsamea* may concede to *P. tremuloides* and *B. papyrifera*, since well-drained fertile soils provide greater opportunity for the recruitment and subsequent re-invasion of less shade-tolerant species (Bouchard et al., 2006). The late arrival of *T. occidentalis* in old boreal stands has been linked to increases in soil organic matter and coarse woody debris, facilitated by the

senescence and decomposition of post-fire cohort trees (Simard et al., 1998; Bergeron, 2000).

Many past studies have relied on chronosequences to examine forest succession. While useful to infer general trends, this approach is increasingly criticized for studying long-term vegetation dynamics as it allows the underlying assumption that all sites along the temporal sequence have developed similarly in their abiotic and biotic components (Johnson and Miyanishi, 2008). Similarly, dendrochronological techniques have also been used to reconstruct stand history (e.g., Johnson et al., 1999; Bergeron, 2000); however, this approach is often limited in systems where tree species decay rapidly after death. Also, high sampling costs often constrain dendrochronological reconstruction to small sample areas and limit inference space. Alternatively, repeated aerial photography in conjunction with surveyors' records has emerged as a valuable tool for studying long-term vegetation change (e.g., Frelich and Reich, 1995; Bouchard et al., 2006). While this method is sometimes limited by low resolution, it can provide a broad temporal and spatial sampling frame for studying forest change in jurisdictions that maintain comprehensive historical archives.

In this paper, we use a methodology for studying population dynamics of boreal tree species based on long-term repeated measurements of stand development, derived from historical aerial photographs and ground surveys. Our objective was to test for trends in individual species abundance over time. Specifically, we sought to test the following hypotheses: 1) Temporal shifts in boreal tree species composition are related to TSF, characterized by decreases in the abundance of shade-intolerant species and increases in the abundance of shade-tolerant species over time; 2) Temporal trends in

species abundance may differ with physical site conditions since species relative competitive ability may be site specific; 3) Commonly occurring intermediate disturbances may alter trends in species abundance over time; and 4) Temporal trends in species abundance may differ depending on initial stand composition due to inter and intra species interaction effects.

4.2 MATERIALS AND METHODS

Study area

Our study was located in region 3E (Hills, 1959) in northeastern Ontario, Canada (see Chapter Three, Fig. 3.1). Mean annual temperature is 1.3°C and mean annual precipitation is 831 mm (Canada Climate Normals 1971-2000, Timmins). Dominant tree species include *P. banksiana*, *P. tremuloides*, *Populus balsamifera* (L.), *B. papyrifera*, *P. mariana*, *P. glauca*, *A. balsamea*, and *T. occidentalis*. The dominant stand-replacing natural disturbance is high-intensity crown fires with a mean fire cycle between 100 to 200 years (Bergeron et al., 2001). Other important natural disturbances include wind throw, and insect infestation by spruce budworm (SBW) (*Choristoneura fumiferana*) and forest tent caterpillar (FTC) (*Malacosoma disstria*) (Fleming et al., 2002; Rich et al., 2007).

Sampling strategy

We sampled 361 stands that were deliberately selected using stratified random sampling to capture a wide range of stand composition, age, and site conditions for fire-originated stands. We established our sampling frame from forest inventory plots that were ground surveyed in 1982 by the Ontario Ministry of Natural Resources (OMNR). To facilitate sampling, we stratified stands into: 1) species-dominant stands, defined as those stands dominated by $\geq$ 50% individual species; and 2) mixed-deciduous or coniferous stands, defined as those not considered species-dominant stand types, but dominated ($\geq$ 50%) by either deciduous or coniferous basal area. For each stand type, we attempted to sample young (< 80 years), intermediate (80-120 years), and old (> 120

years) stands on both upland and lowland sites if applicable. Stands identified as barren and scattered or influenced by harvesting activities were not selected.

Each of the sample stands were then measured four to six times over 8-15 year intervals, encompassing a ~ 60 year time period, by combining ground survey measurements and sequential aerial photo interpretation measurements of each stand. Two measurements were from ground surveys, and two to four were from aerial photo interpretation. The ground survey measurements consisted of the original surveys conducted in 1982 by the OMNR and re-measurements of the same ground surveys completed by us between the years 2000 and 2003. Each ground survey consisted of a fixed 200 m long transect line, along which, 10 variable-radius point samples with a wedge prism (basal area factor two) were established 20 m apart. At each point, live stems > 10 cm diameter at 1.3 m height were counted by species and considered as part of the tree canopy layer (Hayden et al., 1995). Three canopy stems of the dominant species, based on basal area, were selected. Heights and ages of these stems were measured and used to determine the site quality (Plonski, 1974). A soil pit was dug at the fifth point sample of each transect line. At each pit, soil characteristics were determined, including soil texture and moisture regime. Evidence of intermediate disturbances (i.e., wind throw, SBW and FTC infestation) was also recorded for each point sample in each ground survey.

Aerial photo interpretation measurements were done using series of sequential aerial photos taken of the sample stands between 1946 and 1992 (provincial government records). Aerial photos older than 1986 were 1:15,840 scale, while more recent photography was 1:20,000. Photo interpretation was done by a qualified photogrammetry

technician. To interpret the sample stands on the photos, the ground survey transect lines were located, as precisely as possible, on each sequential photo of the target stand. A two hectare rectangular plot (100 x 200 m) was centered on the transect line and stand composition was interpreted within the plot following Zsilinszky (1963). Species basal areas, from photo interpretation, were calculated from % species cover, site quality (as determined from ground surveys), age (corrected from ground survey data to reflect year of photography) and estimated stocking (based on % canopy cover). Photo interpretation and species identification was verified from field checks on the re-measured ground surveys, taking note of what species dominated the snags and dead trees to confirm possible changes in composition through time. Less than four aerial photo measurements were conducted for some stands because the stands were too young (< 20 years old) to be adequately interpreted in the earliest photos (Zsilinszky, 1963). We then combined the two ground surveys and the aerial photo interpretations for each stand to re-construct its developmental history, including changes in tree species composition and disturbance history.

Although both methods have been widely used in forest inventory operations (Husch et al., 2003), differences between aerial photo interpretation and ground surveys may confound observed transitions in stand composition between measurements. To determine the amount of difference, we randomly chose 30 stand plots where measurements of species composition were available from both aerial photo interpretation and ground surveys in 1982. Paired sample *t*-tests were used to determine if a significant difference could be detected. No significant difference was found for *P. banksiana*, *Populus* sp., *B. papyrifera*, and *P. mariana*. However, *P. glauca* was

underestimated by approximately 13%, while *T. occidentalis* and *A. balsamea* were overestimated by 4% and 10% in the aerial photos, respectively. When species were pooled into shade-intolerant and shade-tolerant groups, estimates between the two methods were not significantly different ($P > 0.05$).

Stand establishment date (i.e., time since fire, TSF) for stands < 80 years old was determined from Ontario fire history maps that documented fires > 200 ha between 1921 and 1978 (Donnelly and Harrington, 1978). For older stands, we used tree ages to estimate the date of the last fire (Bergeron, 1991). In the field, the same trees used to determine site quality were also used to determine TSF if they were clearly from the post-fire cohort. *P. banksiana*, *P. tremuloides*, *P. balsamifera*, *B. papyrifera*, and *P. mariana* were preferentially selected as they provide a more precise date of the last major disturbance (Bergeron, 1991). Trees with fire scars that clearly survived fire(s) and were not part of the current age cohort were not sampled. In stands that were dominated only by shade-tolerant tree species such as *P. mariana*, *P. glauca*, *A. balsamea* or *T. occidentalis*, the least shade-tolerant tree species was chosen. When the more shade-tolerant trees were the oldest in a stand, and no fire scar(s) were found on the stems, we assumed that the less shade-tolerant trees were not a part of the initial cohort after fire. The more shade-tolerant trees were then used to determine TSF. Thus, TSF estimates for stands dominated by shade-tolerant species, is an approximation of minimum age of TSF. All increment cores were taken to the pith at breast-height (1.3 m above ground) and brought back to the laboratory. In the laboratory, the cores were mounted on constructed core strips and sanded to make rings visible. Rings were then counted using a hand-held magnifier until the same count was obtained three successive times. Time since fire was

determined by adding 7 years to tree ages at breast height if the stand was dominated by *Populus* sp. or *B. papyrifera*, 8 years if dominated by *P. banksiana*, and 17 years if dominated by *P. mariana* or other shade-tolerant species based on an empirical model developed specifically for our study region (Vasiliauskas and Chen, 2002). Underestimation of TSF is possible when attaining tree age estimates from breast-height measurements, particularly for shade-tolerant species (Gutsell and Johnson, 2002; Parent et al., 2002). When possible, we avoided using *A. balsamea* for estimating TSF (Kneeshaw and Claveau, 2001).

Response and predictor variables

Population dynamics were examined by studying trends in individual species abundances over time for each of the main boreal tree species within our study area, including (in order of increasing shade-tolerance): *P. banksiana*, *Populus* sp., *B. papyrifera*, *Picea* sp., *A. balsamea*, and *T. occidentalis* (Humbert et al. 2007). *Populus* sp. includes *P. tremuloides* and P. *balsamifera*. *Picea* sp. includes *P. mariana* and *P. glauca*. These groupings were made due to difficulty in discriminating these species on the small scale aerial photography (Zsilinszky, 1963).

We prepared two response variables to study species abundances. The first, periodic annual increment (PAI) in basal area, (Δba, $m^2 \cdot ha^{-1} \cdot yr^{-1}$), represents the average annual growth of the target species for the period of years between repeated stand measurements:

$$[1] \qquad \Delta ba = \frac{ba_{i+1} - ba_i}{tsf_{i+1} - tsf_i}$$

where, ba_i is the estimated basal area of the target species at the i^{th} measurement and ba_{i+1} is the estimated basal area of the target species at the next measurement. tsf_i is the corresponding estimated time since fire at the i^{th} measurement and tsf_{i+1} is the estimated time since fire at the next measurement.

Although Δba is useful in inferring increases and decreases in species abundance over time, it does not necessarily indicate changes in the dominance of the target species within the stand. We therefore prepared a second response variable, PAI in relative percentage of basal area, ($\Delta \%ba$, $\%ba \cdot ha^{-1} \cdot yr^{-1}$), which represents the average annual change in the relative percentage of the target species for the period of years between repeated stand measurements:

$$[2] \qquad \Delta \%ba = \frac{\%ba_{i+1} - \%ba_i}{tsf_{i+1} - tsf_i}$$

where, $\%ba_i$ is the relative percentage of basal area of the target species at the i^{th} measurement and $\%ba_{i+1}$ is the relative percentage of basal area of the target species at the next measurement. The relative percentage of basal area for each target species was calculated by dividing the basal area of the target species in the stand by the total basal area for the stand at each measurement.

Initially, PAI was calculated for the 8-15 year periods between repeated stand measurements. However, due to excessive zeros in our data set, caused by frequent instances of no net change in species abundance, we widened the time interval to ~ 60 years, including only the first and last measurement for each stand. For all stands, the first measurements were from aerial photo interpretation and the last are from ground surveys.

To test our main hypotheses, the following predictor variables were created for analysis: mean time since fire (TSF_{mean}), stand type, land class and intermediate

disturbances, i.e., forest tent caterpillar (FTC), spruce budworm (SBW), and wind throw (Table 4.1). Mean time since fire represents the average TSF of the ~ 60 year time period between the first and last measurement for each sample stand:

$$[3] \qquad TSF_{mean} = \frac{TSF_{first} + TSF_{last}}{2}$$

where, TSF_{first} and TSF_{last} represent the estimated TSF at the first and last measurement, respectively, for each stand.

Table 4.1 Predictor variables used in analyzing species abundance.

	Variable	Abbreviation	Type	Units	Proxy for
1.	Mean time since fire	TSF_{mean}	Continuous	Years	Average stand age for periodic increments
2.	Land class	LC	Categorical	LC 1, LC 2	Soil type and moisture conditions
3.	Stand type	Stand Type	Categorical	Conspecific, Mixed-intolerant, Mixed-tolerant	Indicator of initial stand composition
4.	Forest tent caterpillar	FTC	Categorical	Absence, Presence	Disturbance from forest tent caterpillar
5.	Spruce budworm	SBW	Categorical	Absence, Presence	Disturbance from spruce budworm
6.	Wind	Wind	Categorical	Absence, Presence	Disturbance from wind

The stand type variable had two purposes. Firstly, stands that initially contained high abundances of the target species tended to have greater magnitudes of PAI relative to stands in which the target species was only a minor component; mainly, because there were more individual trees of the target species to experience growth (gains in basal area) or mortality (losses in basal area) in species dominant stands. To control for this excess variation we developed stand type as an indicator of initial species abundance at the first stand measurement. Secondly, creating the stand type variable allowed us to test for

species-interaction effects, by permitting examination how PAI of the target species was affected by what species it was initially associated with. Since shade-tolerance is considered a major controlling factor in species abundance throughout succession (Bergeron, 2000), we expected individual species population dynamics to differ depending on whether they were initially associated with species of similar, lower or higher shade-tolerance. Therefore, the stand type variable was summarized into to three categories: 1) conspecific, the target species was initially dominant, i.e., $\geq$ 50% of stand basal area; 2) mixed-intolerant, the target species was initially a minor component (< 50% of stand basal area) mixed with shade-intolerant species; and 3) mixed-tolerant, the target species was initially a minor component (< 50% of stand basal area) mixed with shade-tolerant species. Stand measurements dominated equally by two or more species were classified based on the most shade-tolerant species (Humbert et al., 2007).

Land class was used as a proxy for edaphic conditions, derived from soil texture and moisture measurements at each ground survey. Land class was summarized into two broad categories: 1) LC1, characterized by fine to medium textured soils and moist to wet soil moisture conditions; and 2) LC 2, characterized by medium to coarse textured soils and fresh to dry soil moisture conditions.

Intermediate disturbances were those where up to 75% of the canopy trees were destroyed by a disturbance agent. Stands with > 75% destruction were excluded from our study. The intermediate disturbance variables were each summarized into two broad categories indicating the 'presence' or 'absence' of substantial disturbance within the ~ 60 year time period between the first and last stand measurement. All repeated measurements for each stand were investigated for evidence of insect infestation, from

spruce budworm and forest tent caterpillar, and wind throw damage. Evidence of insect damage was also acquired from insect infestation maps produced annually for Ontario by the Forest Insect and Disease Survey conducted by the Canadian Forest Service since 1941. Insect damage was considered 'present' if there was evidence of approximately three years of infestation between the first and last stand measurement. Spruce budworm damage was the most prevalent form of disturbance, with the last major outbreak in the region occurring between 1972 and 1981. Ninety and 64% of all disturbance damage in *A. balsamea* dominated stands and mixed-tolerant stands, respectively, were caused by spruce budworm defoliation. Wind throw damage was considered present if between 10 and 75% of the trees in the stand were tipped-over or broken off. Several stands showed evidence of minor fire damage, but were excluded from our analysis.

Statistical analysis

General linear models (Kutner et al., 2005) were developed to test whether the two response variables, Δba and $\Delta \%ba$, for each target species, were significantly related to the set of predictor variables using the R statistical language and environment (version. 2.8.1; R Development Core Team 2008). A quadratic term (TSF^2_{mean}), to account for potential curvilinear relationships over time, and all two-way interactions between the predictor variables, were included in the full models. We used manual backward elimination based on *t*-tests (critical value of $\alpha = 0.05$) and change in Akaike's Information Criterion (AIC) scores between the full model and reduced models (Kutner et al., 2005; Dalgaard, 2008) to select the most parsimounous models. A change in AIC of > 2 was considered a substantial change in the descriptive ability of the reduced model over the full (Chatterjee and Hadi, 2006). The manual selection method was preferred

because it allowed us to impose logical constraints on the variable exclusion process (Dalgaard, 2008). Assumptions of normality and homogeneity were assessed by examining normal probability plots and scatter plots of the standardized residuals for each model. Influential data points were evaluated using the DFITS influence test.

Due to inherent multicollinearity that often exists amongst ecological data, overfitted models can result (Graham, 2003). In such cases, valid statistical interpretation of individual variables may be compromised. To address this, multicollinearity measures were calculated for each full model. These included pair-wise comparisons between variables, and Generalized Variance Inflation Factors (GVIFs) (Fox, 2002). Although the GVIFs values for each full model were below the acceptable threshold of 4 (Fox, 2002), our pair-wise comparisons did indicate some interdependency between stand type and the disturbance variables, SBW and FTC. This coupled effect was expected since both disturbance variables are 'species-specific' and are more likely to occur within stand types where their host species are more common. No variables were removed from our models due to multicollinearity, however, coupled effects were cautiously monitored when performing the manual backwards eliminations and when interpreting the effects of each of the variables in the final fitted models.

Model goodness-of-fit was interpreted from R^2 and by evaluating the effect-size measures of the predictor variables retained in the final models (Table 4.2). The effect size of the predictor variables was calculated using Eta-squared, which represents the proportion of total sum of squares explained by each predictor variable in the model (Howell, 2002). The predicted values for each model were plotted against the predictor variables to visually inspect for trends in species abundance.

4.3 RESULTS

Shade-intolerant species

Periodic annual increment of basal area (*Δba*) for *P. banksiana* was positive during early stand development, indicating increases in basal area within the first ~100 years after fire (Figs. 4.1). Because of the significant interaction between mean time since fire (TSF_{mean}) and stand type, for each shade-intolerant species (Table 4.2, Models 1.1), trends in *Δba* differentiated between conspecific and mixed stands, with conspecific stands demonstrating greater magnitudes of *Δba*, but roughly similar trends over time. For *P. banksiana*, *Δba* showed a negative linear relationship with TSF_{mean}, with net losses in basal area beginning around 75-150 years after fire (Figs. 4.1a, b, c). Decline in *P. banksiana* basal area was delayed on dryer, coarser textured LC2 soils ($P < 0.05$; Table 4.2). Trends in *Δ%ba* (Figs. 4.2a, b, c) corroborate the negative linear decline in *Δba*, further signifying that *P. banksiana* abundance steadily diminishes during late stand development.

Populus sp. and *B. papyrifera* both demonstrated curvilinear trends in *Δba* over time, indicating initial periods of basal area growth, followed by net losses, then a second period of increase (Figs. 4.3 and 4.5). Although no significant difference was detected between mixed stand types, with respect to TSF_{mean} and stand type interactions (Table 4.2, Models 2.1 and 3.1), the second increase observed in both species appears most evident in mixed-tolerant stands (Figs. 4.3c and 4.5c). However, conflicting negative linear trends observed in *Δ%ba* for *Populus* sp. (Figs. 4.4a, b and c) are indicative of decreases in relative abundance over time, suggesting only a minor compositional role in the long-term.

Table 4.2 Summary statistics for each model for each target species.

Species	Model	Response Variables	R^2	Predictor Variables			
				Term	*df*	*F*	η^2
P. banksiana	1.1	*Δba*	0.51	TSF_{mean}	1	118.29***	0.20
				Stand Type: *con* [a], *msi* [b], *mst* [b]	2	44.36***	0.15
				Land Class	1	4.15*	0.01
				TSF_{mean} · Stand Type: *con* [a], *msi* [b], *mst* [b]	2	47.40***	0.16
	1.2	*Δ*%ba	0.17	TSF_{mean}	1	4.58*	0.02
				Stand Type: *con* [a], *msi* [b], *mst* [b]	2	15.05***	0.15
Populus sp.	2.1	*Δba*	0.40	TSF_{mean}	1	62.24***	0.13
				TSF^2_{mean}	1	46.16***	0.10
				Stand Type: *con* [a], *msi* [b], *mst* [b]	2	14.24***	0.06
				TSF_{mean} · Stand Type: *con* [a], *msi* [b], *mst* [b]	2	14.88***	0.06
				TSF^2_{mean} · Stand Type: *con* [a], *msi* [b], *mst* [b]	2	11.81***	0.05
	2.2	*Δ*%ba	0.29	TSF_{mean}	1	8.61**	0.03
				Stand Type: *con* [a], *msi* [b], *mst* [b]	2	34.47***	0.26
B. papyrifera	3.1	*Δba*	0.24	TSF_{mean}	1	27.99***	0.08
				TSF^2_{mean}	1	20.15***	0.06
				Stand Type: *con* [a], *msi* [b], *mst* [b]	2	3.47*	0.02
				FTC	1	14.69***	0.04
				TSF_{mean} · Stand Type: *con* [a], *msi* [b], *mst* [b]	2	4.76**	0.03
				FTC · Stand Type: *con* [a], *msi* [b], *mst* [ab]	2	3.04*	0.02
	3.2	*Δ*%ba	0.27	Stand Type: *con* [a], *msi* [b], *mst* [c]	2	38.83***	0.26
				SBW	1	4.91*	0.02
Picea sp.	4.1	*Δba*	0.15	Stand Type *con* [a], *msi* [b], *mst* [c]	2	5.75**	0.03
				Land Class	1	4.25*	0.01
				Wind	1	42.74***	0.11

	4.2	Δ%ba	0.24	Stand Type: *con* [a], *msi* [b], *mst* [c]	2	44.42***	0.22
				Wind	1	10.65**	0.03
A. balsamea	5.1	Δba	0.22	Stand Type [†]	1	32.00***	0.12
				SBW	1	25.47***	0.10
	5.2	Δ%ba	0.18	Stand Type [†]	1	19.12***	0.08
				SBW	1	24.04***	0.10
T. occidentalis	6.1	Δba	0.24	TSF_{mean}	1	14.01***	0.13
				Land Class	1	11.87***	0.11
	6.2	Δ%ba	0.22	TSF_{mean}	1	9.03**	0.06
				Stand Type: *con* [a], *msi* [b], *mst* [b]	2	6.99**	0.09
				Land Class	1	10.28**	0.07

Notes: Abbreviations are: *df*, the degrees of freedom for each predictor variable; *F*, the calculated *F*-statistic for each predictor variable; η^2, Eta-squared effect size measure for each predictor variable.

[a, b, c] are used to signify which levels of the stand type predictor variable significantly differed from one another, where *con* = conspecific, *msi* = mixed shade-intolerant, and *mst* = mixed shade-tolerant stand types.

[†] signifies that the Stand type predictor variable has only two factor levels, *msi* and *mst*.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

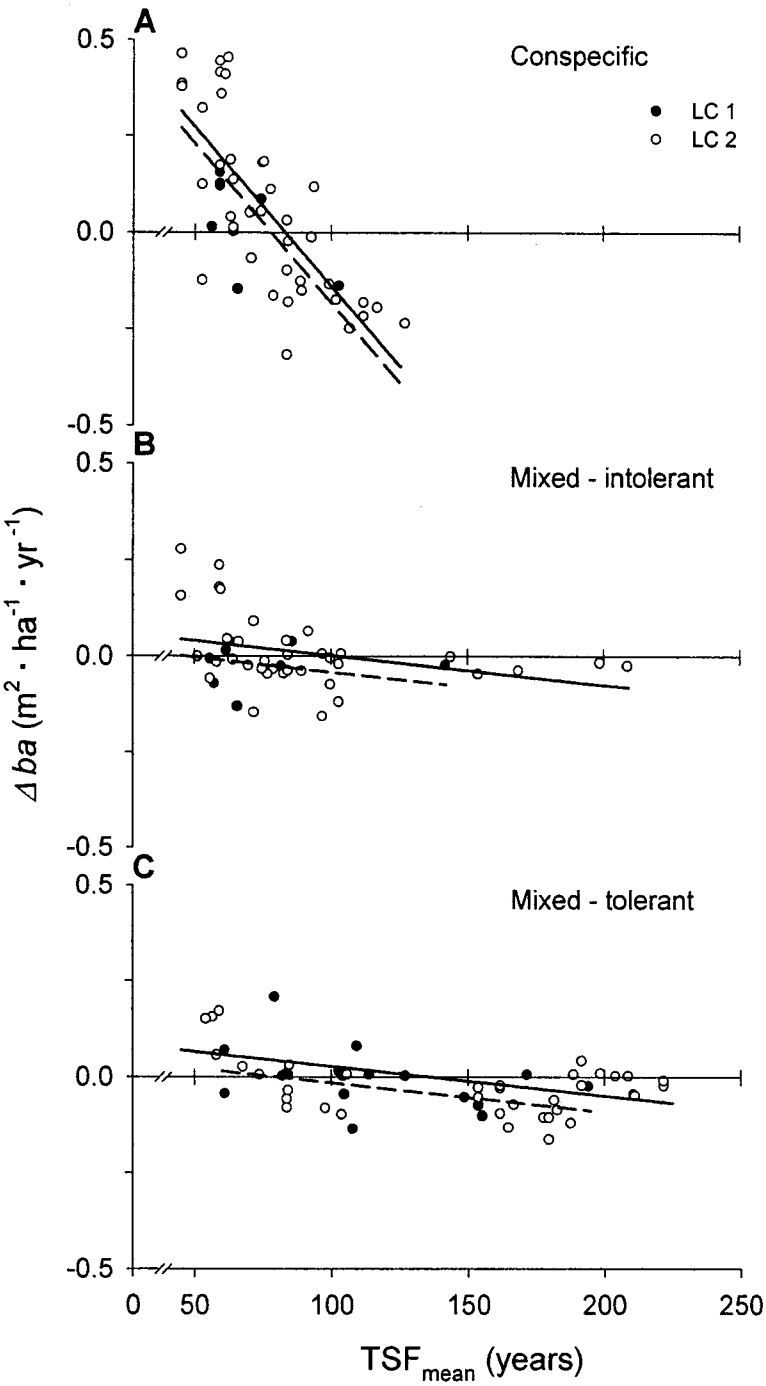

Figure 4.1 Observed data and fitted regression curves for periodic annual increment of basal area for *P. banksiana* as a function of TSF_{mean}, stand type and land class. Dashed line is for LC1 sites and solid line is for LC 2 sites.

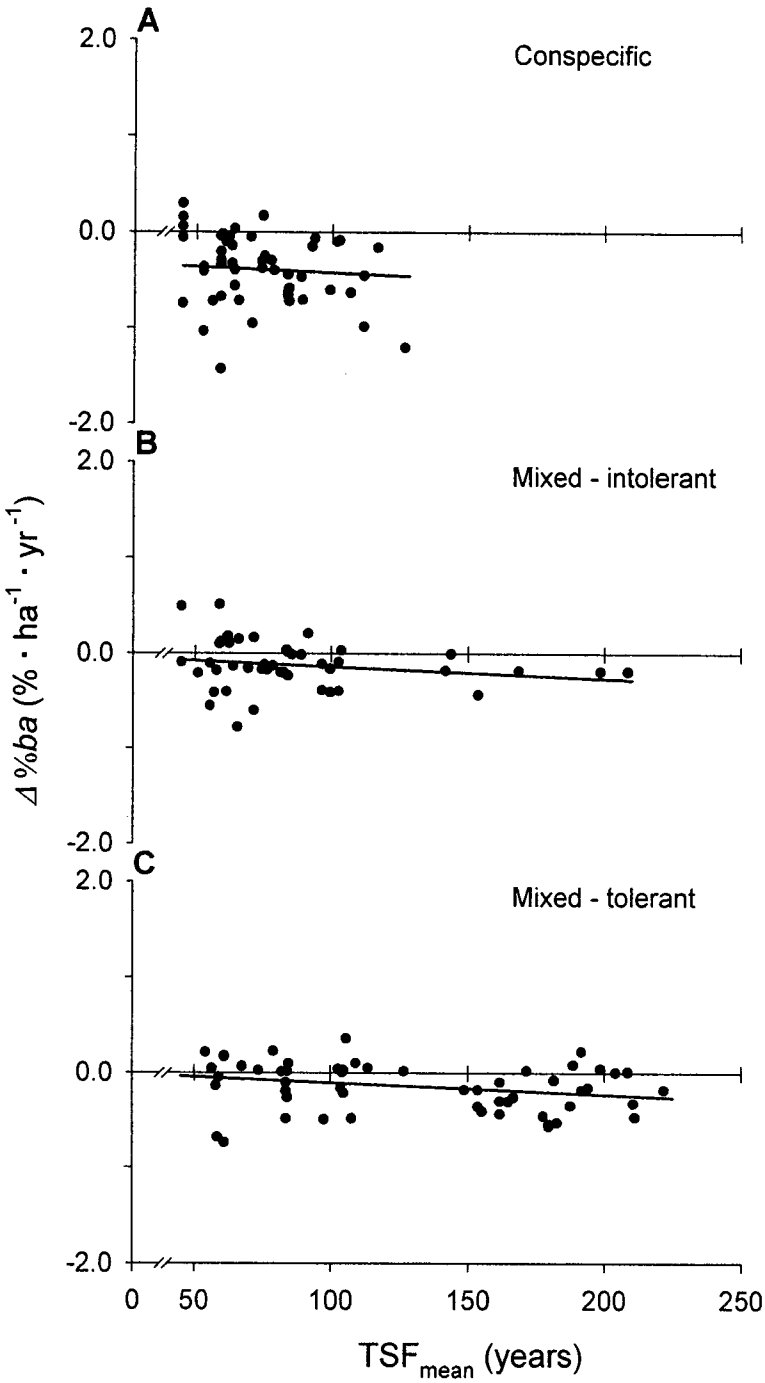

Figure 4.2 Observed data and fitted regression curves for periodic annual increment of relative % basal area for *P. banksiana* as a function of TSF_{mean} and stand type.

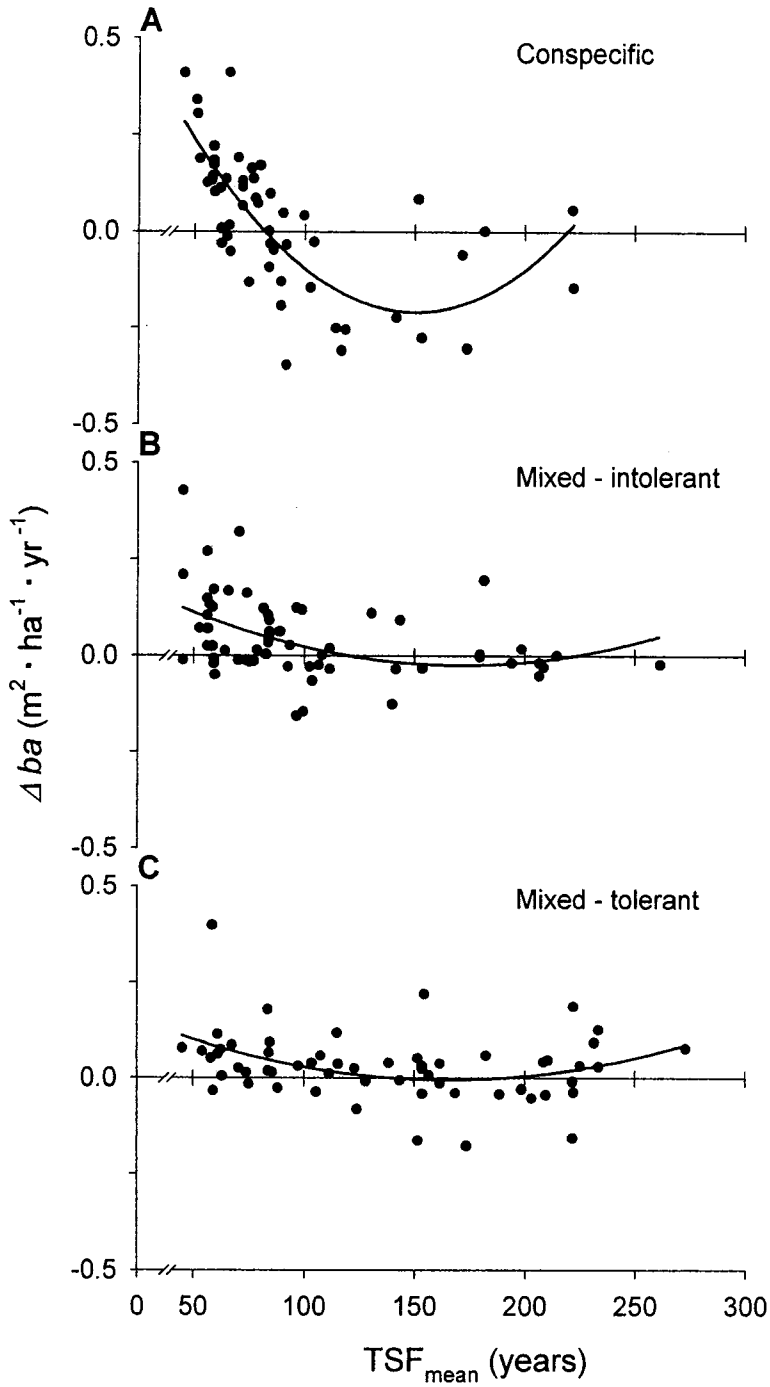

Figure 4.3 Observed data and fitted regression curves for periodic annual increment of basal area for *Populus* sp. as a function of TSF_{mean} and stand type.

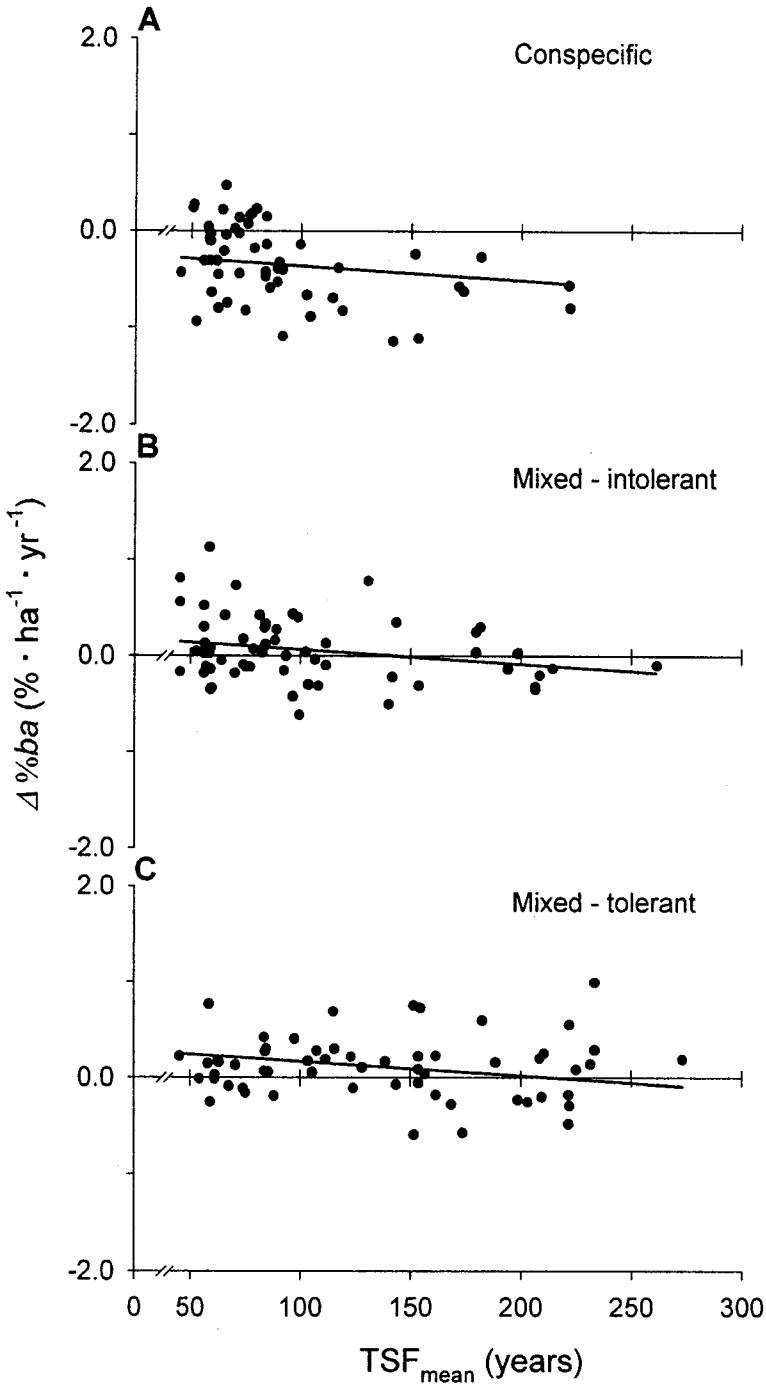

Figure 4.4 Observed data and fitted regression curves for periodic annual increment of relative % basal area for *Populus* sp. as a function of TSF_{mean} and stand type.

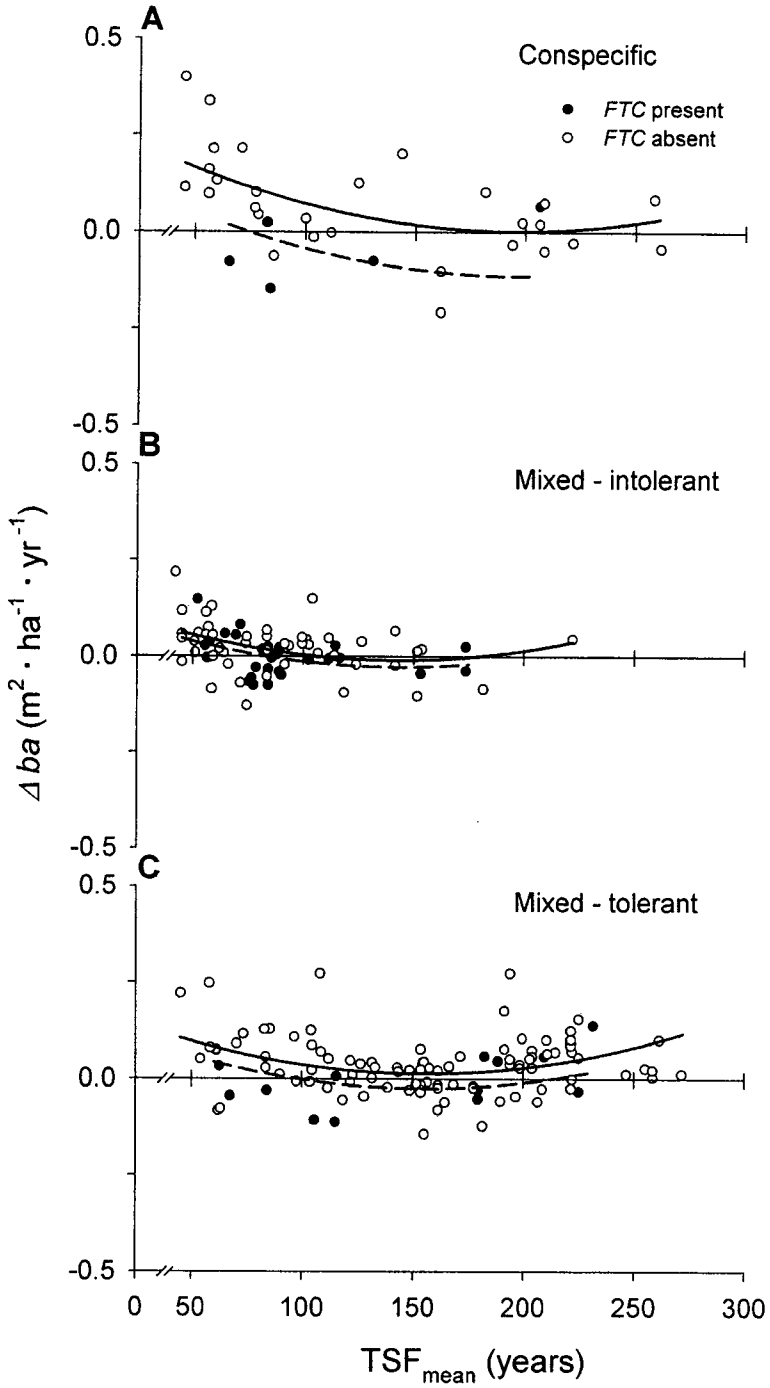

Figure 4.5 Observed data and fitted regression curves for periodic annual increment of basal area for *B. papyrifera* as a function of TSF_{mean}, stand type and FTC. Dashed line is for FTC present and solid line is for FTC absent.

FTC had an overall negative effect on *Δba* for *B. papyrifera*, but no relationship with *Populus* sp. was detected (Table 4.2). Effects from FTC on *B. papyrifera* were related to stand type, with the largest negative impacts occurring in conspecific and mixed-tolerant stands, respectively (Fig. 4.5). No significant relationship between *Δ%ba* and TSF_{mean} was detected for *B. papyrifera*; however, *Δ%ba* of *B. papyrifera* was highest when stand types were disturbed by SBW, with the highest positive response occurring in mixed-tolerant stands (Fig. 4.6).

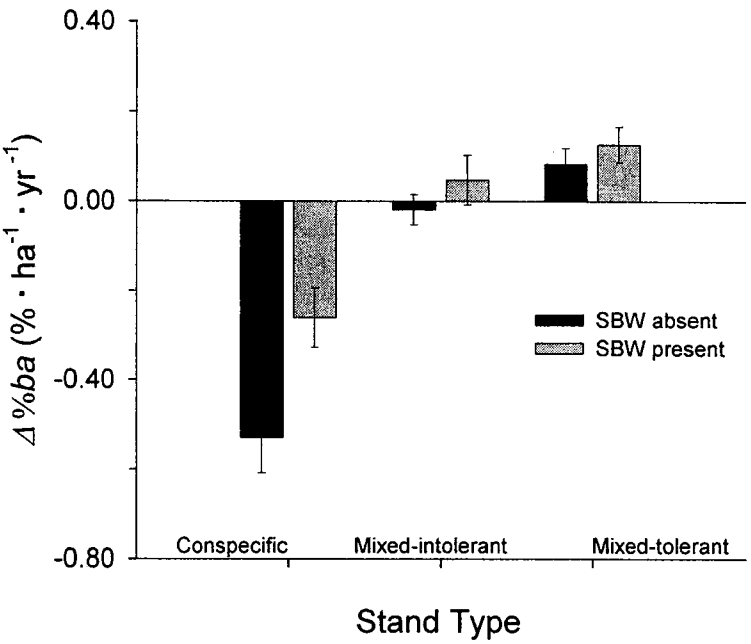

Figure 4.6 Mean observed values for periodic annual increment of relative % basal area for *B. papyrifera* as a function of stand type and SBW. Error bars represent one standard error.

Shade-tolerant species

No significant relationship with TSF_{mean} was observed for *Δba* and *Δ%ba* for either *Picea* sp. or *A. balsamea* (Table 4.2). Rather, the abundance of each species was more explained by intermediate disturbances and site conditions. The *Δba* for *Picea* sp.

was higher on LC 1 sites (Fig. 4.7) ($P < 0.05$; Table 4.2, Model 4.1); however, no relationship between land class and *A. balsamea* abundance was detected. *A. balsamea* was largely affected by SBW disturbance (Figs. 4.9 and 4.10), as outbreaks explained ~10% of variation in both *Δba* and *Δ%ba* (Table 4.2). *Picea* sp. was the only species examined significantly affected by wind disturbance (Table 4.2, Models 4.1 and 4.2). Although no interaction effect occurred between stand type and wind, effects from wind disturbance were greater in magnitude in conspecific stands. For both *Picea* sp. and *A. balsamea*, *Δba* and *Δ%ba* differed among stand types (Table 4.2); both species showed greater overall increases in abundance in mixed shade-intolerant stands (Figs. 4.7, 4.8, 4.9 and 4.10).

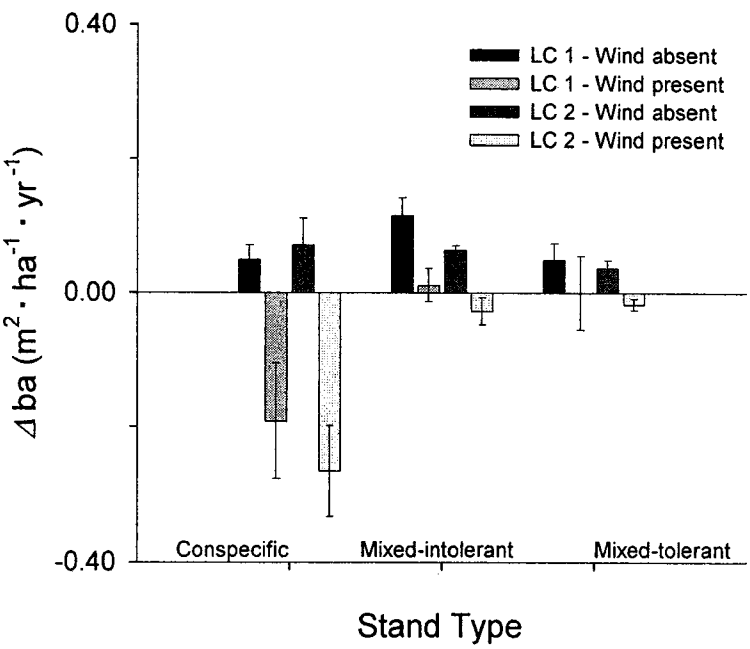

Figure 4.7 Mean observed values for periodic annual increment of basal area for *Picea* sp. as a function of stand type, land class and wind. Error bars represent one standard error.

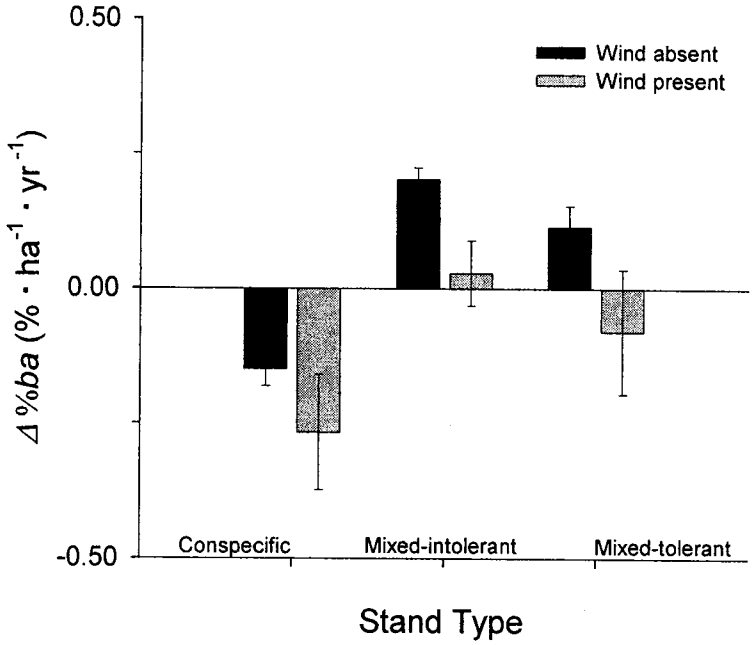

Figure 4.8 Mean observed values for periodic annual increment of relative % basal area for *Picea* sp. as a function of stand type and wind. Error bars represent one standard error.

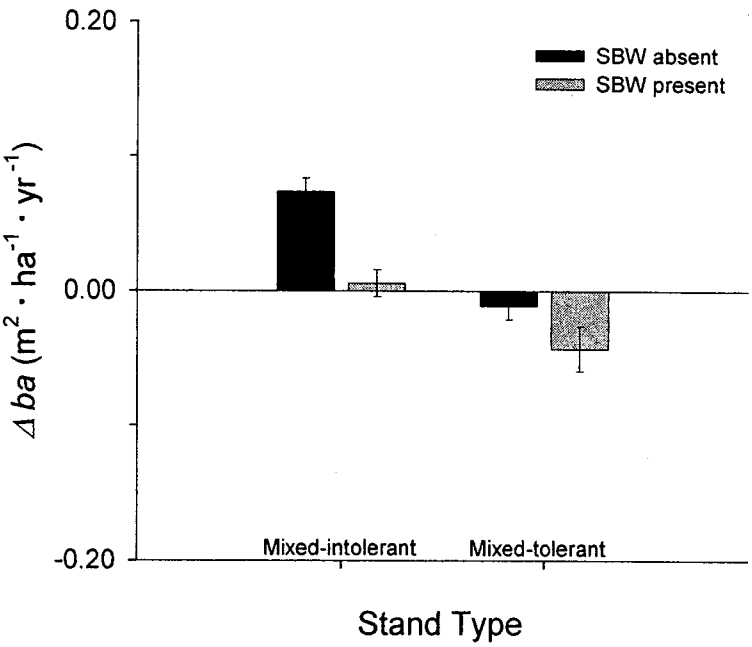

Figure 4.9 Mean observed values for periodic annual increment of basal area for *A. balsamea* as a function of stand type and SBW. Error bars represent one standard error.

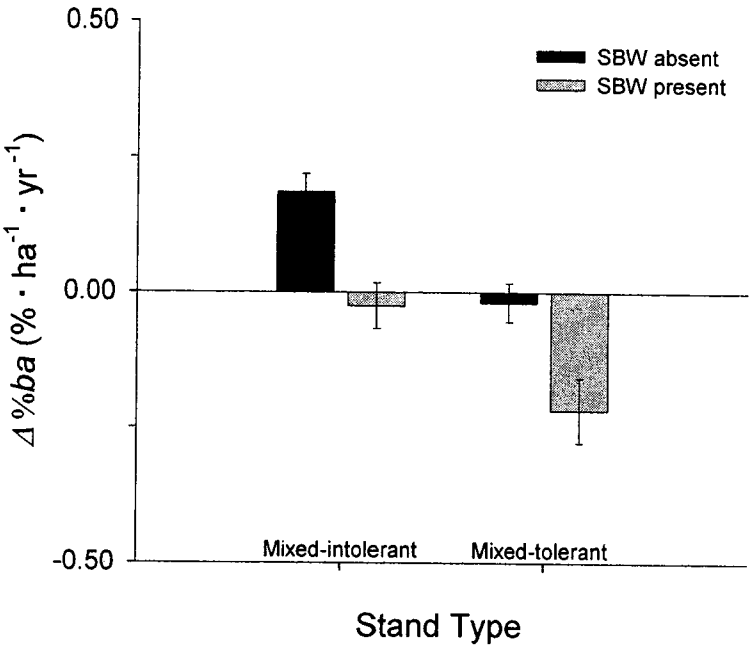

Figure 4.10 Mean observed values for periodic annual increment of relative % basal area for *A. balsamea* as a function of stand type and SBW. Error bars represent one standard error.

Of all species examined, *T. occidentalis* showed the most evident increase in abundance during stand development, with *Δba* and *Δ%ba* having a positive linear relationship with TSF_{mean} (Figs. 4.11 and 4.12); fully contrasting trends observed for shade-intolerant *P. banksiana*. For *T. occidentalis*, *Δba* and *Δ%ba* were also related to land class ($P < 0.001$ and $P < 0.01$, respectively, Table 4.2), with abundance being higher on LC 1 sites, similar to *Picea* sp.

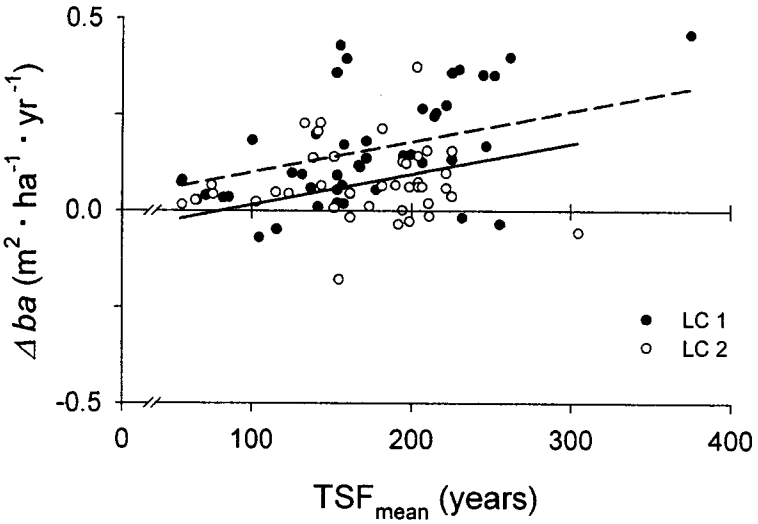

Figure 4.11 Observed data and fitted regression curves for periodic annual increment of basal area for *T. occidentalis* as a function of TSF_{mean} and land class. Dashed line is for LC1 sites and solid line is for LC 2 sites.

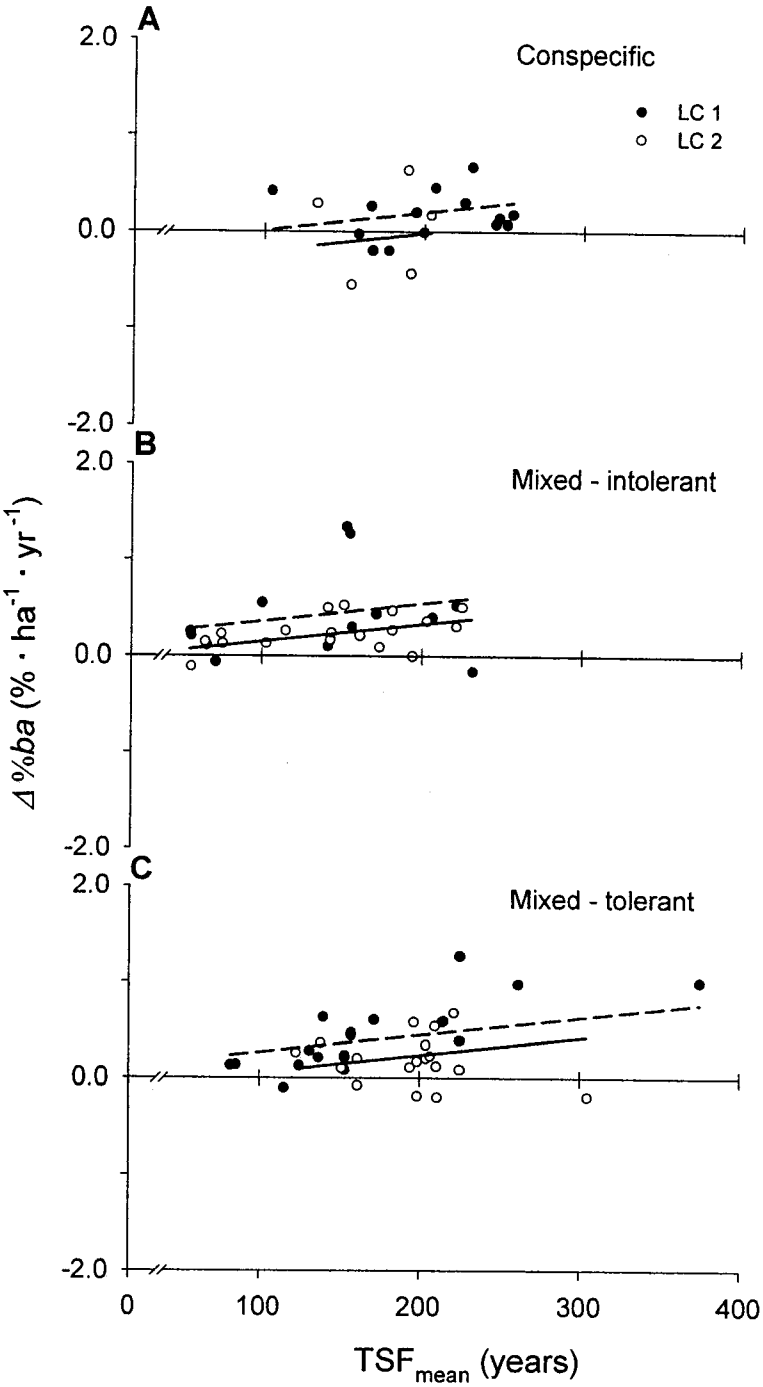

Figure 4.12 Observed data and fitted regression curves for periodic annual increment of relative % basal area for *T. occidentalis* as a function of TSF_{mean}, stand type and land class. Dashed line is for LC1 sites and solid line is for LC 2 sites.

4.4 DISCUSSION

Species population dynamics in relation to TSF

Despite differential species responses to physical site conditions, intermediate disturbances and initial stand composition, the long-term population dynamics of boreal tree species appear largely related to TSF. This is particularly exemplified by our observed trends of *P. banksiana* and *T. occidentalis*, both of which differ substantially in their life history traits and, correspondingly, fulfill alternate successional niches. *P. banksiana* is one of the least shade-tolerant tree species in its native range (Humbert et al., 2007). Although *P. banksiana* is well adapted to colonizing after fire, under natural conditions it does not reproduce vegetatively nor does it typically regenerate under its own canopy (Rudolph and Laidly, 1990). As observed, in the absence of stand-replacing fire it is usually replaced by more shade-tolerant species (Frelich and Reich, 1995). Conversely, *T. occidentalis* demonstrated the most evident increase in abundance in the long-term absence of fire. *T. occidentalis* possesses life history traits conducive to late succession, including very high shade-tolerance, seeding and vegetative reproduction, resistance to insects and pathogens and long life span (Burns and Honkala, 1990). Although the abundance of *T. occidentalis* was slightly overestimated in some of our aerial photograph measurements, the late dominance of *T. occidentalis* corresponds to the delayed establishment noted by Bergeron (2000) who suspected this may be explained by the absence of suitable seedbed substrate directly after fire, and to increased nurse log cover as TSF increased (Simard et al., 1998).

The "U-shaped" pattern we observed for *Δba* in *Populus* sp. and *B. papyrifera* suggests development of subsequent cohorts of each species (Pare and Bergeron, 1995;

Bergeron, 2000). Contrary to *P. banksiana*, *Populus* sp. and *B. papyrifera* may reproduce vegetatively and are known to re-establish within gaps created by the senescence of post-fire cohort trees, thus allowing these species to persist into late stand development under suitable conditions, i.e., sufficient gap size and low competition from more shade-tolerant species (Kneeshaw and Bergeron, 1998; Cumming et al., 2000).

The statistically insignificant relationship between the abundance of *Picea sp.* and TSF may be partially explained by our grouping together of *P. mariana* and *P. glauca*. Both species differ in their life history traits (Wirth et al., 2008). *P. glauca* is generally considered a mid- to late successional species (Simard et al., 1998; Bergeron, 2000). Unlike semi-serotinous *P. mariana*, post-fire recruitment of *P. glauca* is largely dependent on seed dispersal from nearby unburned stands. Increased distances to seed sources and low crop years often delay recruitment and colonization (Wirth et al., 2008). Further, recruitment success of *P. glauca* has been shown to be partially dependent on availability of certain forest floor substrates associated with late stand development, including reduced deciduous leaf litter and increases in nurse log cover (Simard et al., 1998).

The successional role of *P. mariana* is slightly more ambiguous, as its life history characteristics make it suited as both a pioneer and late successional species (Frelich and Reich, 1995). The semi-serotinous cones of *P. mariana* facilitate massive recruitment after stand replacing fire. Its high shade-tolerance, continual seed dispersal and production of new seedlings by vegetative layering allow *P. mariana* to self-replace on a variety of surficial deposits (Lecomte and Bergeron, 2005). *P. mariana* may also invade

older stands and increase in abundance during late succession (Frelich and Reich, 1995; Lecomte and Bergeron, 2005).

Effects of physical site conditions

Although we observed a negative linear relationship of *P. banksiana* abundance over time, decreases in *P. banksiana* appeared delayed on dryer, coarser textured soils (i.e., LC 2 sites). Rudolph and Laidly (1990) and Gauthier et al. (1993) similarly noted that *P. banksiana* may dominate for longer periods on poorer, dryer sites, but be replaced sooner by shade-tolerant species on richer soils. This may be partially explained by differential recruitment abilities among boreal tree species during post-fire development. Provided an adequate seed source, *P. banksiana* is more likely to colonize dry, sandy or gravelly soils relative to other boreal species (Rudolph and Laidly, 1990; Lecomte and Bergeron, 2005) and therefore experience less competition for stand resources. On mesic sites, dense post-fire cohorts of *P. banksiana* inhibit their own ability to regenerate by reducing understory light. Conversely, greater canopy openings and low competition on xeric sites may facilitate self-replacement of *P. banksiana* in the absence of fire (Gauthier et al., 1993).

Greater increases in the abundance of *Picea sp.* and *T. occidentalis* on LC 1 sites may be due to the ability of these species to outcompete other boreal tree species on wet, nutrient poor soils. For the *Picea sp.* group, this effect was more likely caused by *P. mariana*. Many of the LC1 sites that exhibited increases in *P. mariana* and *T. occidentalis* were on wet, organic soil substrates. *P. mariana* and *T. occidentalis* have a high tolerance to increased soil moisture and low nutrient availability and are known to self-perpetuate under such physical conditions (Burns and Honkala, 1990; Wang et al.,

2003; Lecomte and Bergeron, 2005). Their high tolerance to shade and ability to regenerate by seeding or vegetative layering in the understory provides a competitive advantage over other species (Lecomte and Bergeron, 2005).

Effects from intermediate disturbances

The continuation of deciduous species abundance during late succession is largely attributed by gap-forming disturbances, in particular, SBW (Kneeshaw and Bergeron, 1998; Bouchard et al., 2006). This was evident for *B. papyrifera*, as *Δ%ba* was positively related to SBW outbreak, especially in mixed-tolerant stands. Although SBW outbreak was not found related to *Populus* sp. abundance, a coupled effect was detected between Stand Type and SBW, with ~ 50% of mixed-tolerant stands having experienced SBW outbreaks at some time. While no significant difference was detected in *Populus* sp. abundance between mixed-intolerant and tolerant stand types, visual inspection indeed suggests a higher second increase in mixed-tolerant stands.

The degree to which deciduous species will re-establish after SBW outbreaks has been shown to vary considerably, depending on: 1) the relative abundance of deciduous species before infestation, 2) the duration and severity of SBW outbreak, and 3) edaphic conditions (Kneeshaw and Bergeron, 1998; Bouchard et al., 2006). Upper slope stands, dominated by *A. balsamea*, are more likely to change to deciduous composition after severe SBW infestation compared to lower slope stands (Bouchard et al., 2006). Largely, because lower slopes tend to be cooler and less well drained, thus less favorable for deciduous species recruitment relative to *A. balsamea*, *P. mariana* or *T. occidentalis*. Nonetheless, even under suitable post-outbreak conditions, stands are still expected to progress towards shade-tolerant species dominance over time (Kneeshaw and Bergeron,

1998; Bergeron, 2000; Bouchard et al., 2006). Severe outbreaks may destroy mature *A. balsamea* trees, but young regeneration is less likely to be effected (MacLean, 1980). *A. balsamea* are known to form extensive seedling banks under their own canopy. Provided adequate propagules for re-establishment *A. balsamea*, *Picea* sp., and *T. occidentalis* will progressively recruit in the understory, including in gaps too small to cultivate *B. papyrifera* and *Populus* sp. regeneration (Kneeshaw and Bergeron, 1998). Although, *Δba* for *Populus* sp. increased ~ 200 years after fire, *Δ%ba* steadily decreased in all stand types over time. Concurrently, growth in *A. balsamea* and *Picea* sp. abundance was, on average, highest when mixed with shade-intolerant species. Therefore, we suspect outbreaks may facilitate the regeneration of individual deciduous trees or patches of trees, but in the long-term are unlikely to bring succession back to post-fire deciduous abundance levels.

Alternatively, some intermediate disturbances may accelerate succession (Abrams and Scott, 1989; Rich et al., 2007). Canopy defoliation by FTC is commonly considered to promote competing shade-tolerant shrub and conifer regeneration (Chen and Popadiouk, 2002). Our study is the first to demonstrate the negative effects of FTC on the long-term population dynamics of *B. papyrifera*. Curiously, no significant effect was detected for *Populus* sp., which is surprising since *Populus* sp. is commonly considered more susceptible to FTC (Cooke and Lorenzetti, 2006). We propose several explanations for this. Firstly, although no collinearity was detected between Stand Type and FTC, there is likely a coupled effect. Potential variation from FTC outbreaks may have been masked by Stand Type, since FTC is species-specific. Secondly, in areas adjacent to our study, Man et al. (unpublished data, R. Man, T. Scarr and J.A. Rice) reported that after

FTC outbreaks, *P. tremuloides* regeneration was often sufficient to compete with developing shade-tolerant shrubs and conifers. This self-replacement process might also mask effects from FTC.

Wind is another disturbance considered to accelerate succession in the boreal forest (Abrams and Scott, 1989). Generally, shade-intolerant species are considered more susceptible to wind damage because they allocate more resources to rapid growth, rather than structural integrity (Rich et al., 2007). Slower growing shade-tolerant species tend to have denser wood and more compact tree forms. Thus, wind is thought to act as a 'selective weeding' agent on post-fire stands, toppling larger pioneer species and releasing more shade-tolerant species (Rich et al., 2007). Nonetheless, no effect from wind disturbance was detected in our models on shade-intolerant species. Only *Picea sp.* was significantly affected by wind disturbance, having an overall negative impact. This conflicts with the above 'selective weeding' hypothesis, but agrees with many previous reports that mature *P. mariana*, *P. glauca* and *A. balsamea* are very susceptible to wind damage due to their shallow rooting habit and dense foliage (Burns and Honkala, 1990; Steil et al., 2009). We suspect that wind may accelerate succession in mature, post-fire stands of shade-intolerant species, but will actually slow succession in old stands already dominated by shade-tolerant species.

Species interactions effects

Differences between conspecific and the mixed stands types for all species were most likely the result of our methodological design rather than to true species interaction effects (see Materials and Methods section for explanation). For shade-intolerant species, we expected species abundance, during early stand development, to be higher in mixed-

tolerant stands as there would be less competition from other fast growing pioneer species. No such effect was detected for *P. banksiana* or *Populus* sp., but was observed in *Δ%ba* for *B. papyrifera*. However, as no relationship between TSF and *Δ%ba* for *B. papyrifera* was observed, it is difficult to conclude whether this effect was caused by early stand dominance of *B. papyrifera* or subsequent re-invasion in gaps.

Notable differences in growth were detected in *Picea sp.* and *A. balsamea* between mixed-stand types. Both species showed higher overall increases in abundance when associated with shade-intolerant species. Again, no relationship with TSF was observed; thus it is unclear if this effect originated during early or late stand development. We suspect it is related to the greater competitive ability of *Picea sp.* and *A. balsamea* to increase in older stands. Competition for resources is considered the most prominent species interaction influencing species population dynamics during late succession in boreal forests (Frelich and Reich, 1995; Bergeron, 2000). As stands develop, shade-tolerance and regeneration strategy become increasing critical to species continuation as understory light is modified and forest floor properties change (i.e., increased organic matter and changes in soil nutrient regimes). Smaller values of *Δba* or *Δ%ba* for *Picea sp.* and *A. balsamea* in mixed-tolerant stands may be caused by greater competition from associated shade-tolerant species, particularly *T. occidentalis*. In old coniferous stands severely affected by intermediate disturbance, *T. occidentalis* has been shown to out-compete *A. balsamea* and *Picea* sp. (Kneeshaw and Bergeron, 1998; Bergeron, 2000). In fact, we suspect this is why no significant difference was detected in *T. occidentalis* abundance between mixed stand types, as *T. occidentalis* is likely to increase in abundance no matter what other species it is associated with.

4.5 CONCLUSION

In the prolonged absence of stand-replacing fire, trends in individual boreal tree species abundance were detected. As indicated by previous chronosequence and dendrochronological based studies, these patterns may be generalized as a decrease in the abundance of shade-intolerant species and an increase in the abundance of shade-tolerant species with increasing TSF. However, this process does not appear to be simple unidirectional sequence of stages, but rather a complex model subject to differential species responses to such factors as physical site conditions, initial stand composition and intermediate disturbance effects. Species responses to the above tested factors appear largely controlled by shade-tolerance and regeneration strategy. This was exemplified in our results by the most shade-intolerant species, *P. banksiana*, distinctly decreasing in abundance over time, while shade-tolerant *T. occidentalis* increased in abundance. *Populus* sp. and *B. papyrifera*, however, displayed a U-shaped trend in abundance over time, signifying their ability to form subsequent cohorts in old stands under suitable conditions. The abundance of shade-tolerant *A. balsamea* and *Picea* sp. was not related to TSF, but was dependent on intermediate disturbances. We suspect intermediate disturbances play a key role in facilitating the re-invasion of less shade-tolerant species in old stands and are important in maintaining species compositional diversity in old-growth forest.

CHAPTER FIVE: GENERAL CONCLUSIONS

Advances in ecological modeling over the past century have led to a wide variety of methods for modeling forest succession. While a number of reviews have been published on the development of succession models, our review (i.e., Chapter Two) is the first contemporary published review that provides a broad synthesis and description of the methods used to model forest succession and how these may be suited to strategic forest management planning. We found that although qualitative models have formed the basis from which our conceptual understanding of succession originates, their use for today's strategic planning situations is limited to describing empirical observations or theoretical hypotheses. Quantitative modeling methods, alternatively, can be differentiated as empirical or mechanistic. Empirical models rely primarily on direct observational data of vegetation change, while mechanistic models rely on knowledge of the underlying ecological processes that cause succession. Empirical models have been criticized as inflexible and constrictive because they are limited to the quality and coverage of data for formulation, however, mechanistic models are tied to the underlying theory (quality and comprehensiveness) from which they are developed and make the key limiting assumption that the modeled processes they represent are adequately understood. In fact, many algorithms in these models use theoretical relationships based on expert opinion that have not been empirically substantiated. This compromises the overall utility of these models for management purposes and may become a critical issue as global climate change is expected to alter future ecosystem dynamics. It also underscores the continual need for empirical testing of ecological processes that contribute to succession.

In Chapters Three and Four we attempted to fulfill such knowledge gaps by developing a methodology for studying long-term vegetation dynamics in boreal forest ecosystems using a repeated measures experimental design. Our repeated measures dataset was derived from combining sequential aerial photographs and ground surveys for 361 boreal stands over a wide geographical area in central Canada. This data represents a significant advance in the capacity to study boreal forest succession over previously used chronosequence (space-for-time substitution) or dendrochronological reconstruction methodologies. Mainly, because it avoids the inherent assumption of the chronosequnce approach that sites sampled along the temporal sequence have developed similarly in their abiotic and biotic components. Also, because it provides a cost effective approach to studying ecological phenomena over broad temporal and spatial scales – a significant limitation of dendrochronological reconstruction techniques. Further, the use of multinomial logistic regression analysis to test for multiple successional pathways in boreal forest (i.e., Chapter Three) is a new concept that has not been previously applied to North American boreal forest in the published literature.

Using a broad scale approach, Chapter Three provides empirical evidence of the existence of theorized multiple successional pathways in boreal forest. Multiple pathways occured for all shade-intolerant dominated stand types, depending on stand age, edaphic conditions and the presence of intermediate disturbances. Stand types dominated by *A. balsamea*, *Picea* sp., and *T. occidentalis* were more likely to remain constant over time or transition into mixed stands still dominated by shade-tolerant conifers. Only when affected by intermediate disturbances did these stand types demonstrate a reversion back to deciduous dominance. Similarly, by studying individual species population dynamics

(i.e., Chapter Four) we found that stands already dominated by shade-tolerant species will most likely remain as such unless interrupted by disturbance, thus highlighting the key role of intermediate disturbance in maintaining biodiversity in boreal forest systems.

Overall, our results corroborate previous chronosequence-based studies that in the prolonged absence of stand-replacing fire, boreal forests indeed undergo a compositional shift, in which post-fire stands dominated by fast growing shade-intolerant species are eventually replaced by late seral, shade-tolerant species. However, our results also show that this phenomenon is not a simple unidirectional sequence of stages, but rather a complex model dependent on differential species responses to physical site conditions, initial stand composition and intermediate disturbances. Further, individual species responses appear largely controlled by shade-tolerance and regeneration strategy. In fact, we suspect these are the most important life history traits in explaining boreal forest succession.

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APPENDICES

APPENDIX I A DEMONSTRATION OF STAND TRANSITIONS AND HOW STAND TYPES WERE GROUPED BASED ON THEIR PRECEDING MEASUREMENT

Table A1. A hypothetical example of the measurements taken on each stand plot, the data source used to conduct the measurements, the year the measurement is from, and how the stand types observed at each measurement were grouped based on their preceding measurement.

Stand Plot	Measurement	Data Source	Year	Stand type	
1	1	Aerial photo	1949	*Pt*	
	2	Aerial photo	1963	***Pt*** [a]	Transition from *Pt* to *Mc*
	3	Aerial photo	1971	***MC*** [b]	
	4	Ground Survey	1982	*MC*	
	5	Aerial photo	1992	*Pm*	
	6	Ground Survey	2001	*Pm*	
2	1	Aerial photo	1946	*MD*	
	2	Aerial photo	1959	*MD*	
	3	Ground Survey	1970	***MC*** [c]	Transition from *MC* to *To*
	4	Aerial photo	1982	***To*** [d]	
	5	Ground Survey	2000	*To*	
:					
361					

Notes: Stand type abbreviations shown in the table are: *Populus* sp. (*Pt*), *Picea* sp.(*Pm*), *T. occidentalis* (*To*), mixed conifer (*MC*) and mixed deciduous (*MD*).

The bolded measurements, [a] and [b], represent the initial and successive stand types, respectively, observed for measurement three in plot one. In this example, measurement three would be grouped into the *Pt* initial stand type group, and would represent a transition from *Pt* to *MC*. Similarly, the bolded measurements, [c] and [d], in plot two represent a transition from *MC* to *To*. In this case, *To* in measurement four would be grouped into the *MC* initial stand type group.

APPENDIX II THE MAXIMUM LIKELIHOOD ESTIMATES AND STANDARD ERRORS FOR THE INDIVIDUAL LOGITS IN EACH OF THE MULTINOMIAL REGRESSION MODELS

Table A3. Maximum likelihood estimates and standard errors for individual logits in each multinomial regression model.

Model			Logit [a]	Variable	β	SE
1.	*Pb*	i.	*Pm/Pb*	Intercept	-8.36	1.88
				TSF	+0.054***	0.017
				LC	+2.97***	0.98
		ii.	*MC/Pb*	Intercept	-6.55	1.16
				TSF	+0.047***	0.011
				LC	+1.66**	0.78
2.	*Pt*	i.	*Pm-Ab/Pt*	Intercept	-5.57	
				TSF	+0.017**	0.007
		ii.	*MD/Pt*	Intercept	-4.11	
				TSF	+0.015***	0.005
		iii.	*MC/Pt*	Intercept	-4.26	
				TSF	+0.014***	0.005
3.	*Bp*	i.	*Pm-Ab/Bp*	Intercept	-4.51	
				TSF	+0.015***	0.006
		ii.	*MD/Bp*	Intercept	-2.00	
				TSF	+0.002[ns]	0.004
		iii.	*MC/Bp*	Intercept	-3.45	
				TSF	+0.014***	0.004
4.	*Pm*	i.	*To/Pm*	Intercept	-11.74	
				TSF	+0.035***	0.012
				LC	+1.87[ns]	1.2
		ii.	*MC/Pm*	Intercept	-2.25	
				TSF	+0.001[ns]	0.004
				LC	-1.18***	0.41
5.	*Ab*	i.	*Bp/Ab*	Intercept	-2.86	
				DIS	+3.96***	0.9
		ii.	*Pm/Ab*	Intercept	-2.86	
				DIS	+2.35**	1.03
		iii.	*MC/Ab*	Intercept	-1.36	
				DIS	+1.54**	0.71
6.	*To*	i.	*MC/To*	Intercept	-1.72	
				LC	-1.59**	0.76
7.	*MD*	i.	*Pm-Ab/MD*	Intercept	-1.27	
				TSF	-0.004[ns]	0.007
		ii.	*MC/MD*	Intercept	-3.96	

				TSF	+0.016**	0.007
8.	*MC*	i.	*Bp/MC*	Intercept	-3.83	
				TSF	+0.006 [ns]	0.004
				LC	+0.46 [ns]	0.71
				DIS	+1.15**	0.57
		ii.	*Pm-Ab/MC*	Intercept	-2.73	
				TSF	+0.005*	0.003
				LC	+0.73 [ns]	0.51
				DIS	-0.83 [ns]	0.65
		iii.	*To/MC*	Intercept	-5.8	
				TSF	+0.013***	0.004
				LC	+1.80**	0.69
				DIS	+1.11*	0.67
		vi.	*MD/MC*	Intercept	-3.35	
				TSF	+0.002 [ns]	0.004
				LC	+0.14 [ns]	0.7
				DIS	+1.80***	0.54

[a] The initial stand type group serves as the baseline category in each model.
[ns] not significant; * $P < 0.1$; ** $P < 0.05$; *** $P < 0.01$